PHYSIOLOGY OF THE ARTHROPODAN CIRCULATORY MECHANISMS

By N. S. Rustum Maluf
Osborn Zoological Laboratory, Yale University

> "... the circulation of the blood in insects is, in fact, incomprehensible if one supposes that the blood circulates as the result of propulsion by a positive pressure."
>
> —Franck Brocher

CONTENTS

Circulation is necessary for the removal of accumulating metabolites from activated tissues; for a constant and adequate supply of buffers to local regions; for nutrition; for the prevention of an excessive localized rise or fall in osmotic pressure; and, for the carriage of activating substances such as hormones and electrolytes. In arthropods whose blood has a significant respiratory function, the circulation of the blood is also of importance in the transportation of an adequate supply of oxygen to the cells and in the carriage of carbon dioxid from the vicinity of the cells to the respiratory organs. The circulation is of no appreciable respiratory importance in arthropods with a well developed tracheal system.

A. GENERAL ANATOMY

An exhaustive survey of the anatomical contributions to the heart is not attempted. Only important types are selected.

The circulatory system is characterized, except where it is degenerate or absent, by a dorsal muscular tube, or heart, provided with openings, or ostia, and usually extending anteriorly to the brain as the aorta. The ostia are often furnished with valves and are characteristic of arthropods. The heart does not have true chambers, each ''chamber'' of the elongated hearts being indicated solely by a swelling and by the ostial valves. The valves generally direct anteriorly and prevent a reflux of blood. In the larva of the ephemerid, *Cloëon* (Zimmermann, 1880), the posteriormost pair of valves direct posteriorly since the heart, instead of ending blindly at the anal end, as it does in most insects, gives off a single artery into each of the three terminal abdominal cerci. Posterior, lateral, and ventral arteries exist among the Crustacea and Arachnida and always open, often after extensive branching, into the body cavity, or hæmocœle.

''I have also observed,'' wrote William Harvey (1628), ''that almost all animals have truly a heart, not the larger creatures only, and those that have red blood, but the smaller and pale-blooded ones also, such as . . . shrimps, crabs, crayfish, and many others; nay, even in wasps, hornets and flies, I have with the aid of a magnifying glass, and at the upper part of what is called the tail, both seen the heart pulsating myself and shown it to many others.'' This is the first record of the observation of a pulsatile vessel among arthropods.

The heart is always suspended from the integument by connective tissue fibers known as suspensory ligaments. A thin membranous sheet (the dorsal diaphragm or pericardial septum), often fenestrated, containing cells and usually muscle fibers (alary muscles) extends from the ventral surface of the heart to the integument of the dorso-lateral regions, thus separating the pericardial from the visceral sinus. The dorsal diaphragm and its alary muscles were first described by Swammerdamm (1669, pt. I, p. 136): ''All along the course of the heart in the *Cossus,* similar moving fibers are likewise placed, which are inserted into the heart itself; and, they like so many different little ropes, expand and contract it.'' A century later, Lyonnet (1760) called the ''appendages from the heart'' of caterpillars the ''Ailes du Coeur'' but there is no evidence that he believed such to be muscular although one of his celebrated figures shows them as fibrous structures. Straus-Durckheim (1828), in an immortal work crowned in 1824 by the Royal Institute of France, called them the ''oreillette.'' Dogiel (1877) christened the septum and its muscles the ''diaphragm.''

1. *Onychophora* (*Peripatus*). The heart, composed of unstriated and chiefly circular muscle fibers, is a long dorsal vessel running throughout the body length. It has segmentally paired ostia provided with valves. The fenestrated dorsal diaphragm has unstriated alary muscles which run transversely from the cuticle and spread fan-like towards the ventral surface of the heart. There are no arteries (Gaffron, 1885). In most other arthropods the heart and alary muscles are striated. In some insect larvæ the striations are at least not apparent (*cf.* Snodgrass, '35) and probably do not exist (Bergh, '02).

2. *Xiphosura* (*Limulus polyphemus*). The heart (Fig. 8) is elongated and lies in the cephalothorax. It has four pairs of valved ostia, *o*, a corresponding number of chambers, and four pairs of lateral arteries, *la*. Three arteries emerge at its anterior end and subdivide considerably. The dorsal diaphragm is musculated. Because of the large heart and extensive branching and ramification of the arteries (Dohrn, 1871; Edwards, 1872; Patten & Redenbaugh, 1899–'00), *Limulus* has a more highly developed circulatory system than any other arthropod.

3. *Scorpionidea.* The circulatory system of scorpions is very similar to that of their xiphosuran relative. The heart has seven pairs of valved ostia. In contrast to *Limulus,* there is a posterior

aorta in addition to anterior and lateral arteries. The anterior arteries subdivide and communicate with the perineural sinus supplying blood to the lung-"books," or hypodermal folds (Potts, '32).

4. *Araneida.* The heart of spiders has three ostia the largest of which, *i.e.* the anterior one, receives blood from the lung-"books." The posterior and anterior ends of the heart are each attenuated into an aorta. Three pairs of lateral arteries arise from the heart. At its anterior end the dorsal diaphragm forms a pair of open lateral veins through which the pericardial sinus receives aërated blood from the lungs (Causard, 1896; Franz, '03; Willem, '17).

5. *Acarina.* The single-chambered heart (Fig. 1, *h*) has two pairs of ventrally situated ostia and extends anteriorly as an aorta, *ao.* The aorta swells out into a large periganglionic sinus, *pg,* which completely envelops the much consolidated central nervous system, its nerve fibers, the oesophagus, *oe,* pharynx, *p,* and dilator muscles of the pharynx, *dp.* The musculature of the aorta is more sparse than that of the heart. The walls of the sinuses have no muscles. A dorsal diaphragm is absent but dilator muscles extend from the dorsal surface of the heart to the integument (Robinson & Davidson, '13). According to Edwards (1872), a somewhat similar condition exists in *Limulus,* the somatic nerves of which were described as travelling within the arteries.

6. *Tardigrada and Pentastomida.* These minute, free-living forms possess no circulatory or respiratory organs (Huxley, 1878, and Shipley, '09). Movements of the viscera suffice for the circulation of the clear colorless blood which, in tardigrades, evaporates during dry weather and is soon replaced during rain (Shipley). The small size of these animals renders special outfoldings, as extra surface for gaseous exchange, unnecessary owing to their relatively large surface mass ratio.

7. *Pantopoda* (*Pycnogonida*). The heart runs from the level of the eyes to the abdomen. It has two pairs of lateral valvular ostia and sometimes an unpaired one at the posterior end. The fenestrated dorsal diaphragm extends into the distal extremities of the limbs (*cf.* Thompson, '09).

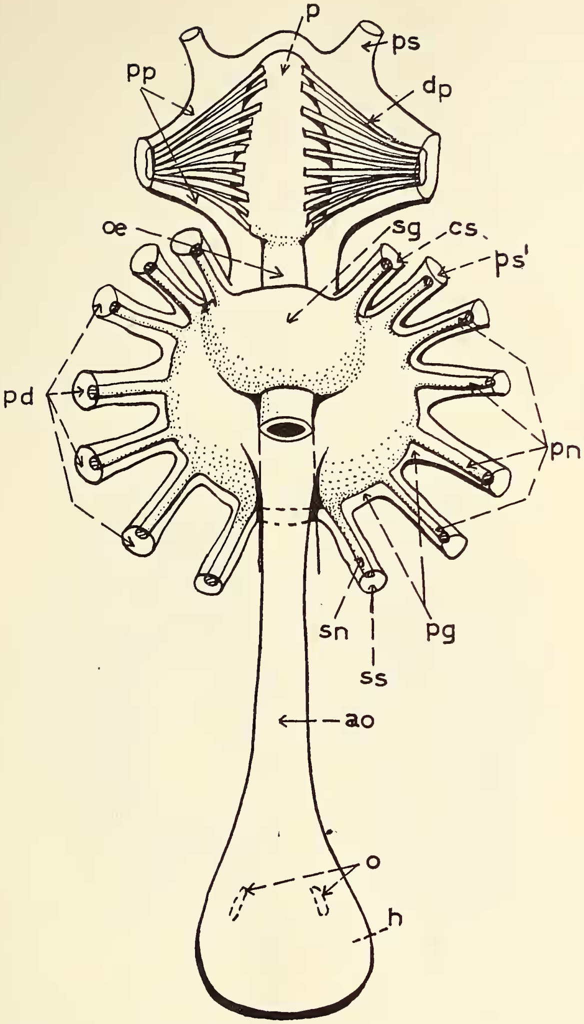

FIG. 1. Dorsal aspect of the circulatory system of the tick, *Argas persicus,* showing related organs. *ao,* aorta; *cs,* cheliceral sinus; *dp,* dilator muscles of pharynx; *h,* heart; *o,* ostium; *oe,* oesophagus; *p,* pharynx; *pd,* pedal sinuses; *pg,* periganglionic sinus; *pn,* pedal nerves; *pp,* peripharyngeal sinus; *ps, ps',* palpal sinuses; *sg,* supraoesophageal ganglion; *sn,* splanchnic nerve; *ss,* splanchnic sinus. (After Robinson & Davidson.)

8. *Crustacea.* The Cirrepedia have no heart. The Entomostraca may have an elongated dorsal vessel with numerous pairs of ostia (*e.g.*, *Branchipus*, *Apus*), or a sac-shaped heart with one pair of ostia (*e.g.*, *Daphnia*) or no heart at all (*e.g.*, *Cypris*). In the Amphipoda the heart is in the thorax and usually has three pairs of ostia. In the Stomatopoda the heart is in the abdomen and is an elongated vessel with several pairs of ostia (Delage, 1881, 1883). It is noteworthy, in this connection, that in the Amphipoda the *thoracic* appendages are transformed into gills while in the Stomatopoda the branchial tufts are borne on the *abdominal* swimmerets. In arthropods with blood gills or lung-"books" the heart is situated in the region of the body whence it can draw aërated blood from the vicinity of the gills as directly as possible.

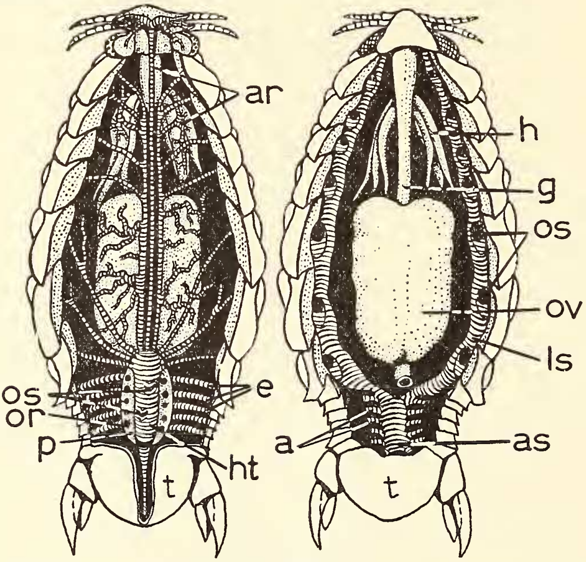

Fig. 2. The isopod *Anilocra mediterranea.* A. Arterial system with the dorsal aspect of the efferent branchial system; dorsal half of body wall removed. B. Venous system with the afferent branchial vessels; heart and arteries removed. *a*, afferent branchial vessels; *ar*, arteries; *as*, abdominal sinus; *e*, efferent branchial vessels; *ar*, arteries; *as*, abdominal sinus; *e*, efferent branchial vessels; *g*, gut; *h*, hepatopancreas; *ht*, heart; *ls*, lateral sinus; *or*, pericardial orifice of an efferent branchial vessel; *os*, ostia; *ov*, ovary; *t*, telson. (After Delage.)

The abdominally situated heart of isopods (Figs. 2 and 3, *ht*) sends several arterial branches anteriorly (Fig. 2A, *ar*) and one posteriorly. Into the otherwise closed dorsal diaphragm, open efferent vessels (Figs. 2A and 3, *e* and *or*) from the gills. There are five pairs of such vessels in *Anilocra mediterranea.* On the floor of the thorax and extending into the head are lateral sinuses (Fig. 2B *ls*) with large ostia, *os*. In the abdomen these sinuses are fused into a single median sinus (Figs. 2B and 3, *as*) which gives off five pairs of afferent vessels, *a,* to the gills. The sinuses and branchial vessels are not mere blood streams but have definite limiting epithelia. There are spaces without tissues surrounding these vessels so that the cylindrical shapes of the vessels would not have been obtained upon the use of injections were it not for the presence of definite walls. The amphipods and læmodipods (*e.g., Caprella*) do not have arteries in the limbs, as the isopods and schizopods do, but have sinus vessels instead.

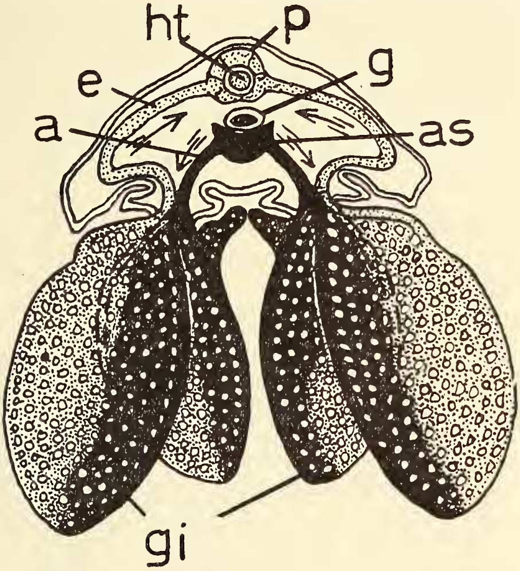

FIG. 3. The isopod *A. mediterranea.* Transverse cut through the abdomen. *a,* afferent branchial vessel; *e,* efferent branchial vessel; *g,* gut; *gi,* gills; *ht,* heart; *p,* pericardium. Arrows represent the direction of flow of the blood. The afferent stream is in solid black; the efferent is stippled. (After Delage.)

Decapods (Fig. 6) and schizopods have branching arteries but no definite branchial or sinus vessels, the blood flowing through lacunar spaces. Although in all cases the heart is attached to the immediately surrounding tissues and dorsal integument by ligaments, it is, in the isopods and amphipods, completely enclosed by the dorsal diaphragm (Fig. 3, *p*). In the læmodipods, anisopods, decapods, and schizopods the dorsal diaphragm does not completely surround the heart but forms a ventral floor to such, as it does in the majority of arthropods. The dorsal diaphragm of the lobster extends into the gills (Fig. 6) as does that of the Pantopoda into the legs, that of the chironomid larvæ into the anal appendages (Fig. 4), and that of the amphipods, *Phronima sedentaria* (Fig. 5) and *Gammarus pulex,* into the locomotor appendages.

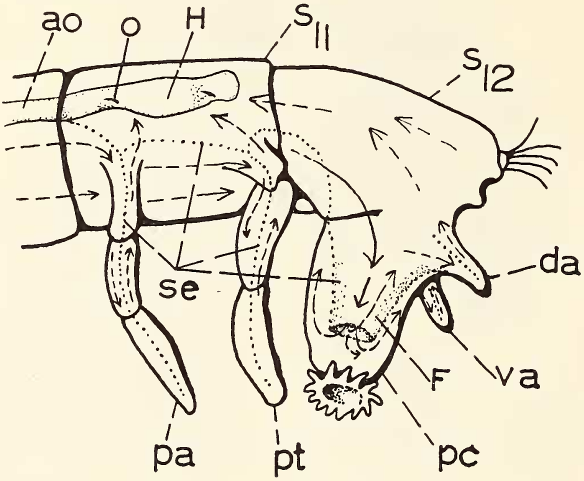

Fig. 4. Left side of the posterior region of the abdomen of a *Chironomus gregarius* larva. *ao,* aorta; *da,* dorsal anal appendage; *H,* heart; *O,* ostium; *pa,* anterior tubule; *pc,* posterior clasper; *pt,* posterior tubule; *S,* trunk segments; *se,* septa; *va,* ventral anal appendage. Arrows indicate the course of the blood. The septa are represented by dotted lines. (After Pause.)

9. *Chilopoda and Diplopoda.* The heart extends throughout the length of the trunk, having ostia in each definitive segment. The branches consist of lateral segmental arteries and an anterior

aorta. A pair of anterior arteries surround the gut and join ventrally to form the supraneural artery (Newport, 1843; Vogt & Yung, 1889–94).

10. *Hexapoda.* With the exception of a few Orthoptera and Apterygota (*cf.* Snodgrass, '35) the heart of insects is restricted to the abdomen where the major portion of the absorptive region of the alimentary tract lies. Since the oxygen capacity of insect

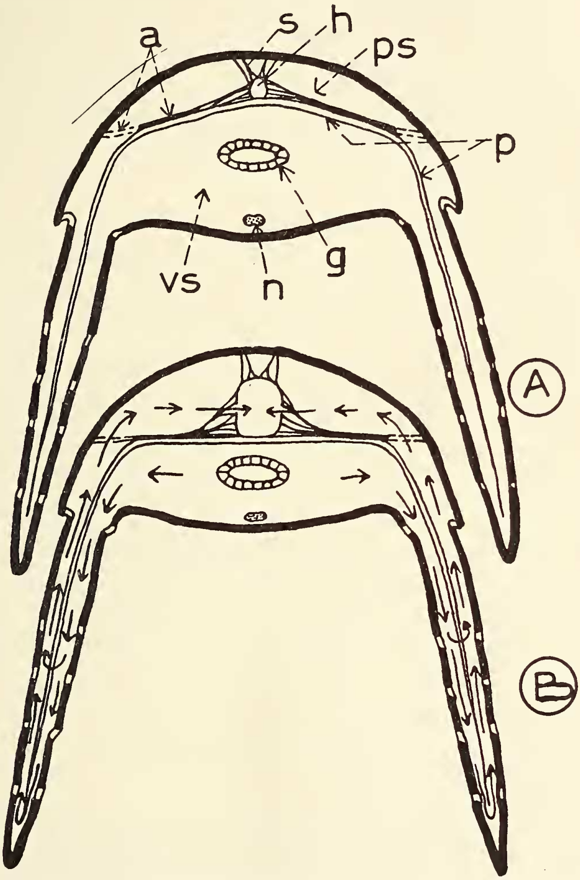

FIG. 5. Schematic transverse section through the thoracic segment of the amphipod *Phronima sedentaria.* A. With heart in the systolic phase. B. With heart in diastole. *a,* alary muscle; *g,* gut; *h,* heart; *n,* nerve cord; *p,* pericardial septum; *ps,* pericardial sinus; *vs,* visceral sinus; *s,* suspensory ligaments. (After v. Haffner.)

blood approximates that of water and may, in fact, be nil (Barratt & Arnold, '11; Bishop, '23; Florkin, '34), the circulation of the blood in these animals cannot be of much respiratory significance but is of nutritive importance. Hence the adaptive advantage of having the ostiated heart in a region as close as possible to the absorptive portion of the gut. The heart extends anteriorly as an aorta (non-ostiated) which often possesses circular muscles such as in the Heteroptera (Maluf, '33). Dorsal diverticula of the aorta occur in some Odonata, Orthoptera, Coleoptera, and Lepidoptera (Brocher, '20; *cf.* Snodgrass, '35). The heart of the water scorpion, *Nepa cinerea* (Hamilton, '31), yields two arteries posteriorly which pass into the muscles of the anal and genital armature. The aorta of the *Corethra* larva is contractile (Tzonis, '36).

The dorsal diaphragm is commonly arched upwards and generally contains muscles fibers. In the honeybee larva (Nelson, '24) it is apparently exceptional in possessing no muscles. These muscles are attached to the ventral surface of the heart and in some forms, such as *Nezara* (Maluf, '33), they cross over to the opposite half of the body. The septum of the dorsal diaphragm may or may not be fenestrated; but there is always a communication between the visceral sinus and the pericardial sinus through the lateral segmental openings. In *Chironomus* larvæ the septum of the dorsal diaphragm extends into the appendages at the posterior end of the trunk (Fig. 4) thus dividing the cavities of the appendages into channels for the inflow and outflow of blood. Pause ('18), probably erroneously, did not consider these septa as pertaining to the dorsal diaphragm and supposed the latter to be completely lacking. In the region of the posterior clasper, *pc,* the diaphragm septum extends as a funnel, *F,* the orifice of the funnel being, presumably, morphologically a fenestrum in the dorsal diaphragm.

The ventral diaphragm is not universally present but is well developed in acridid Orthoptera and the Hymenoptera (*cf.* Snodgrass, '35). In the grasshopper, *Dissosteira,* it extends from the head into the seventh abdominal segment. In the anterior part of the thorax it is a delicate membrane without muscles; posteriorly it has fine transverse fibers which attach laterally to the integument and leave a series of intersegmental openings along the lateral margins of the diaphragm. It contains no cells other than muscle cells and apparently has no supporting membrane.

B. BLOOD PRESSURE AND CIRCULATION

In the early days of microscopical anatomy it was assumed that the "vital fluid" [blood] of the lower animals travels through veins and arteries as it invariably does in vertebrates. Malpighi (1669), the discoverer of the capillaries in vertebrates and hence, virtually, of the closed type of circulation, says this concerning the silkmoth caterpillar: "I have not as yet recognised for certain any arteries, containing the vital fluid, issuing from the heart; sometimes, in a pupa, remarkable segmental branches appeared to me, which I supposed to be arterial trunks." Swammerdamm (1669) believed he knew why he could not observe blood vessels in an *Ephemerus* larva: "No veins or arteries are seen in it for the blood of these insects is of a watery colour, and therefore does not distinguish the vessels containing it from the other parts." Concerning the honeybee larva he writes: ". . . the vessels in it, which carry and return the blood, are so very delicate and transparent, that I was not able to discern them." He injected the heart of a silkmoth larva by blowing a colored liquid into it through a fine glass pipette. "By these means, and then gently blowing into it, the heart and *many of the vessels shooting out from it* [italics mine] may be filled." "The vessels shooting out from it" may have been the tracheæ. Power (1664, p. 59) entertained similar opinions and speaks of the louse as having "a purple Liquor or Bloud, which circulates in her (as the Noblest sort of Animals have;) which though it only be conspicuous in its greatest bulk, at the heart, yet certainly is carried up and down in the Circulatory vessels; which veins and arteries are so exceedingly little, that both they and their liquor are insensible: For certainly, if we can at a Lamp-Furnace draw out such small Capillary Pipes of Glass that the reddest Liquor in the World shall not be seen in them (which I have often tried and done) how much more curiously can Nature weave the Vessels of the Body. . . ."

It was a time before zoologists could conceive of an open blood-vascular system. Thus, some of the best morphologists in Europe, such as Audouin & H. M. Edwards (1827, 1827a), A. M. Edwards (1872), and R. von Hertwig ('00) believed that the circulation of *Limulus* and decapod Crustacea is closed. Even as late as 1911 Leontowitsch remarked that the circulation is the insect, *Ranatra,* and the shrimp, *Palæmon,* is closed although he stated: "Without microscopical preparations it is difficult to determine if these passage-ways (for the blood) are capillaries or merely body lacunæ." Identical observations had been noted by Leeuwenhoek (1688) on scorpions and crabs. Similar apologetic statements were made by Audouin & Edwards (1827) and Edwards (1872) as regards the "veins" of Crustacea and *Limulus*: "The walls of the vessels are of an excessive tenuity . . . only at their termination at the venous sinuses is it possible to recognise that they have an independent existence. . . ." They believed that the veins from the limbs enter the sinuses. Patten & Redenbaugh (1899–'00), in their classical work, could find no veins in *Limulus.* Lund (1825) was one of the first to state that decapod Crustacea possess no veins. In attempting to explain the manner of circulation in the limbs of insects, Louis Agassiz (1851), in a paper that became translated into French, stated that the notion that the tracheae are normally filled with air is only a relic of the times before William Harvey when men believed that undissolved air permeated the ciculatory of vertebrates.

While Hertwig (*loc. cit.*) may not have implied a closed circulation in the morphological sense, he wrote that "the highly localised respiration implies an essentially (*nahezu*) closed blood system." In this he was right. Thus, by means of injection, Baron Cuvier (1805), one of the past master morphologists of Europe, found, in decapod Crustacea and a branchiopod (*Squilla*) that the blood leaves the heart to the different parts of the body; then to the large trunk sinuses; from the sinuses to the gills; and from the gills to the heart. He also showed that the blood entering the heart must first pass through the gills (hence the position of the heart in the vicinity of the gills and the fact that the pericardial diaphragm offers orifices only to the blood leaving the gills); that the blood can enter a gill solely by way of its ventral "vessel"; that the blood traverses the gill blade to its dorsal "vessel" and hence directly to the heart (Figs. 3, 6, and 7). These results were confirmed by Audouin & Edwards (1827) and Plateau (1880). The former also showed that the ventral[1] "vessel" of a gill does not open into the heart but believed that the dorsal "vessel" does. They must, however, have mistaken the dorsal diaphragm for the heart, the description of the dorsal diaphragm of an arthropod appearing in print one year later (p. 229). Otherwise, their description is correct if the term lacunæ is substituted for "vessels." The significance of the aspirating action of the arthropod heart in drawing blood from the gills is now significant and is an excellent substitute for a double circulation and a heart which drives blood almost exclusively by propulsion. In the gills of the crab, *Maia* (Dubuisson, '28), there is only a 6 mm. of water difference between the blood pressure in the cephalothoracic visceral sinus and the pericardial sinus.

1. *Pressure.* When it became known that, among arthropods, the arteries open freely into the body cavity the problem of the mode of circulation through the narrow and elongated limbs became acute. In a closed blood-vascular system it is easy to see how blood can be kept in continuous motion solely by positive pressure. In mammals at least (Starling, '20, p. 946), expansion, *per se,* of the heart is a negligible factor in determining the rate of blood flow since the intraventricular pressure is never negative. Among arthropods the situation is quite different. "The mechanism of the circulation of the blood in insects," wrote Brocher ('31), "is, in fact, incomprehensible if one supposes that the blood circulates as the result of propulsion by a positive force. It becomes easy to understand once one realises that the flow of blood is the result of an aspiration and that in the body of insects this liquid is normally under a negative pressure." Brocher ('20, '31) has noted that, in general, the blood flow of insects is under negative pressure except in regions close to the orifice of the aorta. Contrary to what happens in animals in which the blood passes through definite vessels under a positive pressure, incisions through most regions of the integument cause either

---

[1] Their terms of "external" and "internal" for dorsal and ventral, used in this paper, apply only to arthropods with erect gills (Fig. 6) and not to those with dangling gills (Fig. 3).

no continuous hæmorrhage or no hæmorrhage at all. In many cases (*e.g.*, in leg stumps of a crayfish or insect) if a drop of water is placed on the wound the drop is drawn in. Both Hollande ('11, '11a) and Rabaud ('22) observed that the drop of blood which oozes out during the bleeding reflex of certain insects is frequently reabsorbed through the region of rupture.

On no account, however, should it be supposed that the blood pressure is always negative. Since arthropods have an open blood-vascular system, compression of the integument (produced by contraction of skeletal muscles) causes an augmentation of the blood pressure. Thus, the intra-abdominal blood pressure of dragonfly larvæ (Shafer, '23) shows abrupt changes (18–87 mm. of water) due to variations in the activity of the abdominal skeletal muscles. Molting is, partly in this manner, made possible. Inflation of the gut, either by the swallowing of air or water following molting raises the blood pressure and thus makes feasible the expansion of the wings (Schafer, *loc. cit.*). Locomotor activity can increase the blood pressure in the ventral sinus of crabs to an extent of 10 mm. of water (Dubuisson, '28). The blood in the pericardial sinus is always under positive pressure and puncturing this region sometimes results in death due to loss of blood (*cf.* Herrick, '09, for the lobster). Plateau (1880) inserted a glass tube vertically through the carapace of decapod Crustacea into the pericardial sinus without allowing the escape of a single drop of blood. The column of blood in the tube immediately rose to a height of 16 mm. Once the maximum height in the tube was attained it remained invariable except for certain regions in the pericardial sinus where it alternately rose and fell through an amplitude of 1 mm. synchronously with the heart beat. In the spider-crab, *Maia* (Dubuisson, *loc. cit.*), the pericardial blood pressure fluctuates between 21 and 25 mm. of water. These values are very much lower than those in the arteries of vertebrates.

In limbs supplied with arteries, such as in *Limulus,* the blood is under a positive pressure in the arteries as shown by profuse bleeding upon cutting. The blood pressure in the limbs of certain Crustacea (Picken, '36) is 30–20 cm. of water. As it leaves the arteries, the blood is aspirated from the limbs during diastole.

The blood, in limbs provided with arteries is, hence, under both positive and negative pressure. The aspirating action of the heart during diastole is the major factor in producing circulation especially in forms which do not have a well developed arterial system, and these are the majority. This will become evident under the next topic. The arterial pressure of the lobster (v. Brücke & Satake, '12), measured in the aorta in the region of the third or fourth abdominal segments, attains a maximal, or systolic, value of 170 mm. of water; and a minimum, or diastolic value, of 147 mm. of water. In the crab, *Maia* (Dubuisson, *loc. cit.*), this pressure fluctuates around 55 mm. of water and, of course, diminishes with distance from the heart. It is, however, incorrect to suppose with Dubuisson that this pressure remains positive until the blood returns to the pericardial sinus if by "positive" is implied a flow which is the result of propulsion instead of aspiration.

Because arthropods have an open circulation Wigglesworth ('34) has pointed out that their blood pressure is capable of performing important mechanical functions such as hatching, molting, and wing expansion. "The coiled proboscis of Lepidoptera is extended by means of blood pressure created in the stipes of each maxilla" (*cf.* Snodgrass, '35; Schmitt, '38). That the expansion of the wings soon after eclosion is produced by a localised rise in blood pressure was first recognized by Swammerdamm (1669, pt. I, p. 119) regardless of his explanation for the rise in pressure: ". . . these wings are so swiftly expanded, and yet have neither muscles or joints in them, but only artificially plaited or folded. . . . This difficulty surely is worthy to be solved. . . . I think the water, which is warmer on the surface than in the bottom of the river, flowing all over and penetrating into the wings, in order to promote this needful expansion, may be impelled with greater force, in the same manner as we see the blood is, by the help of hot water, drawn more plentifully into the feet, and those parts are more distended when any one is blooded in the foot. . . . Wherefore we likewise observe that in the wings of insects, if wounded at that time, there follows a mortal hæmorrhage, or if the creature survives, the wings are never afterwards displayed." Swammerdamm, in common with other biologists of his time, did not recognize the haemolymph of insects as blood and thought it to be water.

2. *Circulation.*—a. *Pantopoda.* Although these animals do have a heart, both Carpenter (1854) and Thompson ('09) observed that, especially in species with a small body and exaggerated legs, movement of the blood is produced more by action of the limbs and contractions of the intestinal cæca, which extend into all the locomotor appendages, than by impulses generated by the heart. In fact, Carpenter believed that they possess no specific circulatory organs.

b. *Tardigrada.* Since these minute animals have no circulatory system, movements of the viscera and integument must be adequate in producing blood circulation.

c. *Scorpionidea.* Blood is aspirated into the ventral sinus as a result of the contraction of the muscles attached to the ventral diaphragm. When these muscles relax the ventral diaphragm collapses and blood is thus forced into the lung-"books" whence it is aspirated into the heart as a result of the expansion of the heart muscle. The heart then contracts and propels the blood into the arteries (Potts, '32). Judging from anatomical details, the circulation of the blood in spiders (Clarapède, 1863; Causard, 1892; Wagner, 1893; Willem, '17), *Limulus*, and scorpions is similar.

d. *Crustacea.* Like the Tardigrada, Crustacea without a heart must depend on movements of the viscera and integument for blood circulation. Amphipod, stomatopod, and decapod Crustacea generally have a well developed circulatory system.

Prior to the work of Audouin & Edwards, Latreille (1831), Desmarets (1825), and, in a later work, even Cuvier (1817) succumbed to the notion that the blood enters the gills directly from the heart. This is apparently a relic from Willis' (1674) *De Anima Brutorum* in which it is stated that, during diastole, the heart receives blood from the gills and the "vena cava" (*i.e.,* a mixture of aërated and unaërated blood) and discharges such, during contraction, to the gills and the anterior region of the body. It is of historical interest that Willis drew his conclusion after injecting "a black fluid" into the heart of lobsters.

The most comprehensive work on the circulation of the blood in the Crustacea is that of Delage (1881, 1883). In the isopods the blood is drawn into the ostia of the thoracic sinuses (Fig. 2, *os*) from the body lacunæ, is carried to the abdominal sinus and then, through the afferent vessels (Figs. 2 and 3, *a*), to the gills and aërated (Fig. 3, *gi*). It is then aspirated into the pericardial sinus (Figs. 2 and 3, *p*) and thence into the heart, *h*. All this blood flow is the result of aspiration generated by the heart muscle during diastole. The two walls of the gills are, in many places, confluent (Fig. 3), thus check the rate of blood flow through such, and hence offer a greater length of time for gaseous exchange. The telson of isopods acts as a gill in the same manner. In the læmodipods and amphipods the afferent vessels to the limbs of the thorax and abdomen all come from the sinus system and not, as they do in isopods, from the arterial system. The end result in both cases is, however, quite evidently the same as far as circulation is concerned. In the Anisopoda the carapace folds are transformed into gills, and, as in the gills of other forms, constrictions are formed by the confluent walls of the carapace. During the zœa stage of macrurous decapods there is a similar carapace-branchial system prior to the appearance of the gills.

The pericardial septum of the amphipod, *Phronima sedentaria* (von Haffner, '33), passes into the thoracic legs (Fig. 5, *p*) and thus allows the existence of afferent and efferent blood streams. During systole (Fig. 5A) the heart propels the blood into the head and abdomen. During diastole (Fig. 5B) blood is forced through the limbs by the aspirant action of the heart and pericardial sinus. A similar condition holds for the amphipod *Gamarus pulex* (Klövekorn, '34).

In the decapods, as exemplified by the lobster or crayfish (Fig. 6), blood is propelled into the ambulatory appendages through the limb arteries, *la,* during systole (circulation by propulsion is shown by broken arrows). During diastole blood is drawn from the gills, *gi,* by suction (circulation by suction is shown by continuous arrows) into the pericardial sinus and heart.

How does the blood circulate through the arborous gills of decapods? We have already noted that each gill stem is fully separated into two channels by the pericardial septum (Figs. 6 and 7, *p*): an afferent channel, *a,* and an efferent channel, *e.*

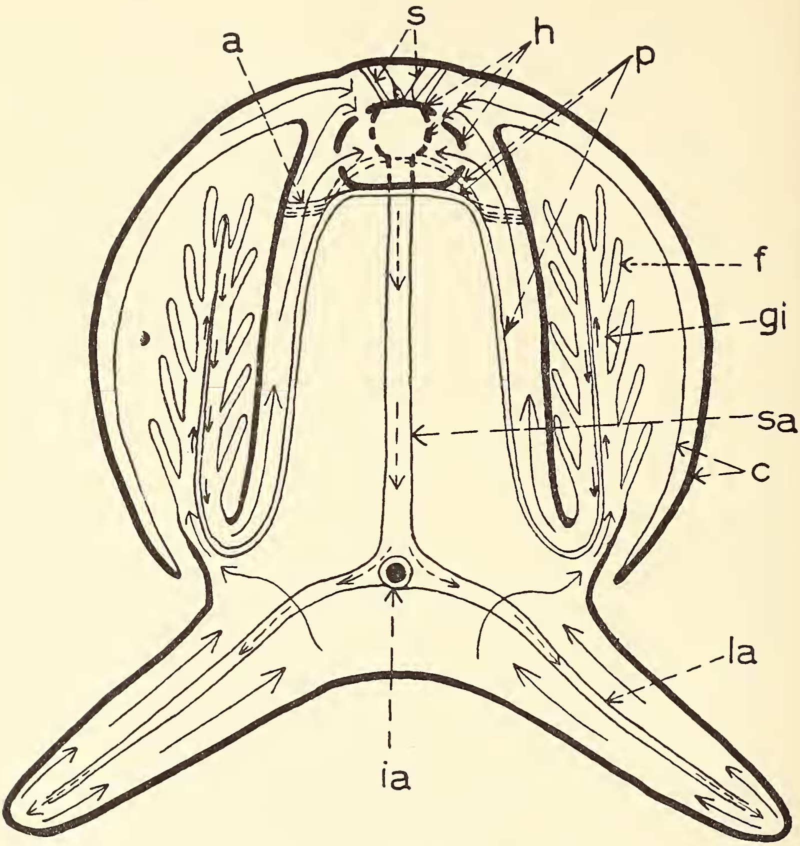

FIG. 6. Transverse section through the thorax of a crayfish. *a*. alary muscle; *c*, fold of carapace; *f*, gill filament; *gi*, gill stem; *h*, heart (small round interior one in systole; the large outer one in diastole); *ia*, inferior artery; *la*, limb artery; *p*, pericardial septum or dorsal diaphragm (position during systole shown by broken line); *s*, suspensory ligaments; *sa*, sternal artery.

Each gill filament, *f*, is also longitudinally divided into an afferent and an efferent channel (Fig. 7). There are many circular vessels in the walls of the gill stem some of which, *c*, open into the efferent channel of the gill stem and others into the afferent channel of the gill stem. The afferent channel in each gill filament communicates with an afferent circular vessel while the efferent channel of the gill filament communicates with an

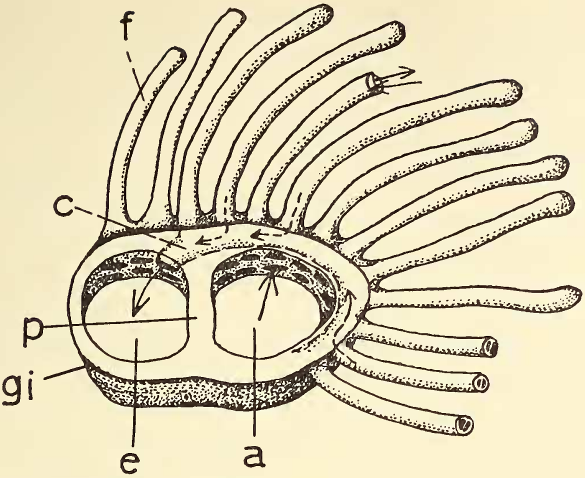

FIG. 7. Diagram of a transverse section through the gill of a lobster showing the course of the circulating blood (arrows). *a*, afferent channel of gill stem; *c*, circular vessel in which efferent channels of the gill filaments open; *f*, gill filament; *gi*, gill stem; *c*, circular vessel in which efferent channels of the gill filaments open; *f*, gill filament; *gi*, gill stem; *p*, extension of the dorsal diaphragm. Each filament communicates with the afferent channel of the gill stem on the one hand and with the efferent channel of the gill stem on the other. (After Herrick.)

efferent circular vessel. Blood which circulates through the gill stem must, therefore, imperatively pass through the gill filaments before reaching the heart.

In the daphnid, *Leptodora kindtii* (Gerschler, '10), there is a pulsatile vessel in the basal segment of each first leg and attached to the integument by ligaments. An innervated muscle passes from the integument to the wall of the vessel and causes its expansion. *The fact that the walls of the vessel are not muscular is proof that the main action of the vessel is aspiratory.*

e. *Hexapoda.* In the honeybee (Snodgrass, '25) blood from the thorax passes through the narrow abdominal peduncle and enters beneath the ventral diaphragm. The backward pulsations of the ventral diaphragm cause some of the blood to flow posteriorly. At the same time, the aspirating action of the heart during diastole causes the blood to enter the visceral sinus by way of the lateral intersegmental openings of the ventral diaphragm.

The blood in the visceral sinus receives food material from the intestine and is drawn into the pericardial sinus and then into the lumen of the heart through the ostia of the latter. During systole the blood in the heart is propelled anteriorly and enters the hæmocœle beneath the brain.

The circulation of the blood in the posterior region of the trunk and limbs of chironomid larvæ (Fig. 4) is very similar to what occurs in the regions of the gills and appendages of Crustacea in which the pericardial septa enter the gills or limbs. Afferent and efferent channels in the legs and antennæ have also been noted by Carus (1830) in beetles, by Moseley (1871) in cockroaches and by Leontowitsch ('11) in *Ranatra.* The latter was an adherent of the closed circulation theory and hence believed that the ascending and descending currents occur through definite blood vessels. Meyer ('31) has made the most extensive study of the afferent and efferent channels in the limbs of insects (various species of larval ephemerids). He noted that the longitudinal septum contains nuclei and divides a limb completely, being attached to the inner ends of the hypodermal cells. The septum is not a prolongation of the pericardial septum into the legs since it ends proximally at the coxa. Tracheæ and muscles, however, ensure that the blood from the efferent channel (in the outer longitudinal half of a limb) enters the pericardial sinus.

Circulation in the limbs and wing veins may also be produced by accessory hearts whose action is chiefly aspiratory. Carus (1830) was the first to describe the circulation in the wings and noted that, in beetles, the blood always flowed out in the anterior margin of the wing and back in the posterior margin. Moseley (1871) made similar observations on the cockroach, *Blatta,* and beetles and pointed out that the blood vessels of the wings cannot be looked upon merely as tracheal sheathes since the tracheæ are very small in comparison and do not enter the transverse connecting branches. He suggested that the wings probably act as lungs and that the absence of these "aërating" organs in the female cockroaches is compensated for by the much larger size of the salivary glands of the latter—which were also supposed to behave as lungs (see also Mr. A. Hollis, to whom Moseley refers).

Yeager & Hendrickson ('34) confirmed, in the adult cockroach, *Periplaneta americana,* the observations of Carus and Moseley. In the larval wing pads, however, the former observed that the "blood flows centrifugally in all the main veins, including the vannals; these streams turn medially and become centripetal with respect to the posterior border of the tergum. . . ." Moseley had noted that, under conditions of exhaustion, the current in the posterior margin of the hind wing of the adult cockroach may be reversed—the circulation thus evidently reverting to the immature condition.

In the cockroach (Yeager & Hendrickson, *loc. cit.*) "part, at least, of the blood from the elytra and wings passes into the heart cavity through the mesotergal and metatergal pulsatile organs, respectively." The same may be said for ants (Janet, '06), honeybees (Freudenstein, '28), dragonflies, wasps, moths, grasshoppers and beetles (Brocher, '16, '31), and various mayfly adults (Bervoet, '13; Meyer, '31). This is effected by the aspirating action of the pulsatile organs (Meyer). The average velocity in the subcostal cell of a cockroach elytron is 34.3 mm./min. (Tauber & Snipes, '36). In *Dytiscus* and *Aeschna* (Brocher) the lumina of the pulsatile ampullæ communicate with the lumen of the aorta; in *Sphinx* (Brocher) and in *Apis* (Freudenstein) there is no communication. In the two-winged insects, or Diptera, and in a certain ephemerid, *Cloëon,* having only a single pair of wings (mesothoracic) only the mesothoracic organ exists (Zimmermann, 1880; Popovici-Baznosanu, '05; Drenkelfort, '10; Meyer, '30). Thompsen ('38) has, however, noted a pair of pulsatile organs in the mesothorax of the domestic fly and also one in each wing. There is no direct connection between these vessels and the aorta. Those in the thorax begin to function in the pupal stage while those in the wings act only after the outfolding of the wings.

Janet and Freudenstein believed the tergal organs to be muscular plates which are attached to the integument laterally. On the other hand, Zimmermann, Brocher, and Meyer (*loc. cit.*) have described such as sac-like ampullæ. The contractions of these organs may be regular (Meyer) or irregular (Zimmermann) and are not synchronous with or dependent on the heart beat (Brocher

'16, Freudenstein, and others). Most of the ampullæ have ostia, but those of the ephemerid, *Heptagenia* (Meyer), appear to be exceptional since no blood flow into such could be observed. Circulation of blood in the wings is necessary for the deposition of pigment in such (Tenenbaum, '34).

In the adult dragonfly (Whedon, '38) there is an aortic diverticulum to the lumen of the axillary cord of each wing. Blood, which is propelled to the anterior (costal) "veins" of the wings by the contraction of the heart and leaves the aorta, is drawn through the wing "veins" into the axillary cord.

Pulsatile organs have been noted in the legs of various species of aquatic Hemiptera and other insects (Behn, 1835; Locy, 1884; Leontowitsch, '11; Crozier & Stier, '27b; Thompsen, '38; and others), and have been found to occur in between the bases of the antennæ of ants, bees, and cockroaches (Pawlowa, 1895; Janet, '11; Brocher, '16, '22; Freudenstein, '28). Since they occur in the path of the efferent blood stream (Leontowitsch) it is clear that their action is chiefly aspiratory. The organs are attached to the integument by passive ligaments and, unlike the organs in the fore-legs of a daphnid (see above), they apparently have no extrinsic muscles. Blood currents in the legs of the Hemiptera are dependent on the organ as shown by their cessation when the organ stops. Locy observed that the rate is irregular and is always faster than the heart rate in a given individual. Not only is the rhythm of the vessels independent of the heart but also the rhythm of one vessel is independent of that of the contralateral half in the intact animal (Locy, 1884; Crozier & Stier, '27b). In contrast to Locy, Crozier & Stier found that the rate of pulsation in any one leg of *Notonecta* is remarkably uniform at a given temperature although individual variation was considerable.

3. *Bodily motions associated with the heart beat.* In spiders (Willem & Bastert, '17) the abdomen, the appendages (when free), and the flexible regions of the integument respond to the small changes in blood pressure by undergoing pulsations of small amplitude synchronously with the heart beat. The lung-"books" perform like a harmonica. In *Limulus* (Tait & Berrill, '36), too, the rhythmic volume change of the gill-"leaves" occurs

in precise *tempo* with the heart beat and "derives presumably from changes in blood pressure"; and the dilation of the heart is coincident with the elevation of the gill-"plates" (Edwards, 1872). The to-and-fro movements of the gills, however, *i.e.*, the respiratory movements proper, are not dependent on changes in blood pressure partly because they will continue even after the heart and blood are removed (Hyde, '06). In the larvæ of certain mayflies (Meyer, '31) the volume of the legs increases during systole and decreases during diastole.

C. THE HEART BEAT

1. *Role of the alary muscles and suspensory ligaments.* A cardiac muscle must be stretched beyond a certain minimum if it is to contract vigorously. The alary muscles which are attached to the dorsal surface of the heart and laterally to the integument, are necessary if the heart is to beat with its normal amplitude although their section does not necessarily result in a cessation of the rhythmic beat (Plateau, 1880; Snodgrass, '35; Dubuisson, '29, '30; Izquierdo, '31; Maluf, '35). Swammerdamm (see above) believed that they expand and contract the heart.

Since the heart is attached dorsally to the integument by means of the suspensory ligaments, the alary muscles must, during diastole, stretch the heart muscle and thus increase the energy of contraction (Starling's "law of the heart," '20, p. 1003).

Carlson ('04–'05b, '06, '07a) had observed that, when the heart of *Limulus* was quiescent due to exhaustion and when the arteries were ligated and the heart was perfused under slight pressure, a series of beats was produced. These effects, however, resulted only when the cardiac ganglion was intact. Increasing the pressure up to a certain unspecified limit augmented the amplitude, tonus, and rate. The same effects were produced by stretching the suspensory ligaments or by attaching opposite hooks to the middle region of the heart. These results were confirmed by Dubuisson ('30, '30–'31a) and Heinbecker ('33) with the exception that they could obtain the same effects on the deganglionated heart. It is possible that Carlson had used hearts of unhealthy animals. The effect of loss of blood and, hence, of internal cardiac pressure on the decrease of the heart rate of Crustacea was nevertheless well known to Carlson ('06).

A certain degree of stretch is necessary for the automaticity and rhythm of the hearts of all invertebrates (Hoshino, '25; Dubuisson, '29, '30; Heinbecker, '33) and although the free excised hearts of some arthropods may beat spontaneously for some time when placed in a perfusion medium (Hunt, Bookman, & Tierney, 1879; Plateau, 1879; Cosmovici, '25; Rijlant, '32; Carlson, etc.) they come to rest prematurely, *e.g.*, the lobster heart (H., B., & T., *loc. cit.*). In the dragonfly, *Agrion,* and the beetle, *Hydrophilus* (Dubuisson, '30), section of the alary muscles causes an immediate stoppage of the heart beat. This is, however, not generally true (*cf.* foregoing authors) provided, of course, that the heart is placed in a balanced perfusion medium. When the heart of the larva of the dragonfly, *Anax junius,* or of the bug, *Belostoma flumineum* (Maluf, '35), is carefully removed from the body wall it generally ceases to beat instantly although there may be a few quivers when it is in a state of collapse. The suspensory ligaments are thus necessary for heart function in these forms—that is, provided the perfusion pressure is not artificially raised. The term "isolated heart" in the paper of Yeager & Hager ('34) must not be taken in its strict sense since the dorsal integument, alary muscles, and suspensory ligaments were kept intact. The same applies to the work of Brocher ('17), Lévy ('28), and Koidsumi ('31) on insect hearts. In fact, as far as I know, a contracting isolated insect heart has never been maintained over any protracted period. The reason for this is probably merely due to difficulties in maintaining a perfusion pressure in such small hearts.

Certain authors, such as Popovici-Baznoșanu ('05) and Dezsö (1878), believe that the pericardium is passive in its effect on the increase in heart volume during diastole. In fact, Dezsö contradicted Dogiel (1877) by stating that the pericardium of the crayfish is not musculated. On the other hand, Dubuisson ('29) seems to have shown that the sudden unusual heart stops which occur, every now and again, during the diastolic phase of certain midge larvæ (*Chironomus dorsalis* and *C. plumosus*) are due to a relaxation of the alary muscles and thus to a release of the heart muscle from a point of critical stretch. He logically concluded that arthropods which do not show such pauses, such as adults of the above, always have their alary muscles in a state of quasi-contraction. He recognized a point of critical stretch at which the effects on the energy of contraction were all-or-nothing. It is disconcerting to know, however, that the heart of the *Corethra* larva (Tzonis, '36) pauses in systole.

2. *Innervation.*—a. *Onychophora and "Myriapoda"* have a ganglionated median dorsal nerve cord (Gaffron, 1885; Lang, 1891) similar to that of *Limulus* and many Crustacea.

b. *Xiphosura.* The gross structure of the cardiac nervous system of *Limulus* (Fig. 8) has been studied by Carlson ('04–'08) and, in detail, by Edwards (1872) and, as to its minute structure, by Patten ('12) and Heinbecker ('33). The term "ventricle" in Heinbecker's paper really implies the heart. The intrinsic innervation consists mainly of a ganglionated median dorsal nerve cord (Fig. 8, *m*), or cardiac ganglion, which is connected with the stomatogastric nervous system by a pair of branches (Edwards, 1872). There are more ganglion cells in the middle region of the cardiac ganglion than in the anterior or posterior regions. The cells are of three kinds (Patten): 1. Small multipolar cells forming a thick irregular covering around the ganglion. In the first three or four segments these cells are few. 2. Giant bipolar cells, not present in the first three or the last segments; give off large branching collaterals. 3. Small bipolar cells; not numerous; found in the first three or four segments. All the ganglion cells increase greatly in number with age, while those of the Crustacea

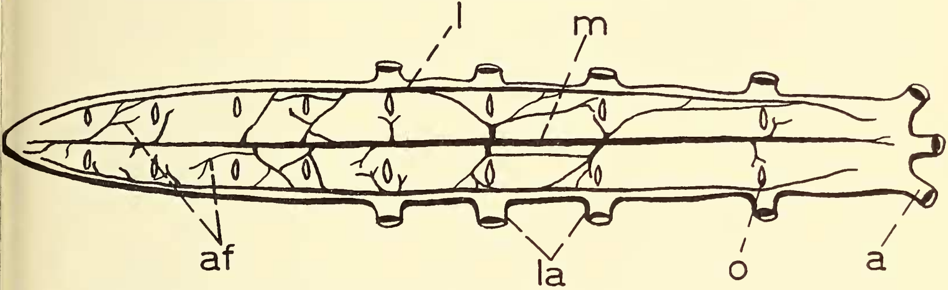

Fig. 8. Dorsal aspect of the heart of *Limulus* with the anterior end to the right. *af,* afferent nerve fibers; *a,* artery; *l,* lateral cardiac nerve; *m,* median cardiac nerve cord; *o,* ostium. (After Carlson.)

and insects, on the other hand, remain approximately constant. No ganglion cells exist in the heart of *Limulus* outside of the median cord (Carlson, '08; Patten, '12), although the radiating branches which connect the cardiac ganglion to the lateral nerves (Fig. 8, *l*) contain a few ganglion cells at their roots (Patten, Heinbecker). Afferent nerve fibers, *af*, pass to the cardiac ganglion from every region of the heart.

The cardio-inhibitor nerves arise from the brain (Carlson, '05) and decrease the rate and amplitude but not the tonus of the beats (see also Hoffmann, '11a). For the following reasons, Carlson suggested that the action of the inhibitor nerves is not exerted directly on the heart muscle but rather on the cardiac ganglion:

1. "The inhibitor nerves enter, not the heart muscle, but the nerve cord on the dorsal side of the heart in the region of the second and third pairs of ostia.
2. "The response of the heart to direct stimulation when quiescent in prolonged diastole, due to strong stimulation of the inhibitor nerves, is similar to the response of the heart to the same stimulus after extirpation of the cardiac nerve cord. Complete inhibition thus simply means the throwing out of function of the median cardiac nerve cord.
3. "Atropine, nicotine, and curare . . . paralyse the inhibitor mechanism of *Limulus* only when they come in contact with the ganglion on the dorsal side of the heart.
4. "If the inhibitor nerves pass from the cardiac nerve cord to end in the heart muscle it ought to be possible to produce inhibition by stimulation of these fibers on their course from the nerve cord to the muscle. This is never possible. Contraction only is produced then."

Heinbecker (*loc. cit.*) found that when the inhibitor ("vagus") nerves are cut the heart beats more rapidly. "The chronotropic responses are naturally inferred to act directly on the large ganglion or pacemaker cells. But, inasmuch as the small ganglion cells have been shown to have an autochthonous rhythm independently of the large ganglion cells it follows that, in order that the heart be stopped by intrinsic fibers these must also act on the small ganglion cells." Stimulation of the inhibitor nerves causes a decrease in the production of CO_2 by the cardiac ganglion (Garrey, '20b). Inhibitor stimuli applied to the cardiac ganglion (Asher & Garrey, '30) decrease the O_2 consumption rate of the same (Dann & Gardner, '30).

The cardio-augmentor nerves arise from the abdominal ganglia and reach the heart together with the inhibitor nerves (Carlson, '05). The fact that the farther posteriorly the location of the stimulus the fewer the augmentor nerves stimulated indicates that the true origin of the fibers is in the anterior part of the central nervous system.

c. *Scorpionidea.*—Here, too, there is an intrinsic elongated dorso-median cardiac ganglion (Police, '02; McClendon, '12; Rijlant, '33a) which has the same functions as that of *Limulus* (Rijlant, '33a). A branch of the stomatogastric nervous system innervates the heart (Police, '03) and possibly, as in *Limulus,* connects with the cardiac ganglion.

d. *Araneida.* The electrical activity of the heart of spiders (Rijlant, '33) is so similar to that of *Limulus* that it suggests that the heart of spiders has a similar ganglionic system. The heart of a tarantula (Carlson, '05–'06a) receives augmentor nerves from the suboesophageal complex.

e. *Crustacea.* Probably the most systematic studies made on the innervation of the crustacean heart are those of Alexandrovicz ('32, '32a, '34) on isopods, stomatopods, and decapods and of Suzucki ('35) on decapods and isopods. In all cases there is a ganglionated nerve cord running along the dorsal surface of the heart. The cells are always few in number. Thus, the cardiac ganglion of the hermit crab, *Aniculus aniculus* (Suzucki), has but ten large multipolar cells while that of the isopod, *Tylos granulatus* (Suzucki), has but six multipolar cells in a row. There are never any ganglion cells at the ventral surface of the heart (see also Newmywaka, '28). Nerve cells in the walls of the crustacean heart had been described by Berger (1876), Deszö (1878), Yung (1878), Dogiel (1877, 1894), Plateau (1880), and Nusbaum (1899); but Claus (1878) and Pogoschewa (1890) were apparently the first to recognize that these cells are generally connected to form a chain. In the prawn, *Palaemon* (Nusbaum, 1899), the ganglionic cells are not connected into a chain but rather form a nerve net. In the crayfish, *Astacus fluviatilis* (Newmywaka, *loc. cit.*) there is no median cardiac ganglion but there is a short transverse ganglionated chain which branches out, the branches, too, containing ganglion cells. There are no ganglion cells in the arteries of decapod and stomatopod Crustacea according to Alexandrowicz ('12–'13) but Nusbaum (*loc. cit.*) states that he found ganglion cells in the subneural artery of *Palaemon.*

As to the extrinsic innervation, the compound thoracic ganglion, or complex, of decapods and stomatopods gives rise to both the augmentor and inhibitor nerves. The inhibitor nerve of *Palinurus* (Carlson, '04–'05, '05–'06a) arises near the origin of the nerve to the third maxilliped of its side (see also Dogiel, 1877). The cardio-augmentor nerve of the same animal arises near the nerve to the first ambulatory appendage of its side. A similar condition holds for the stomatopods and other decapods judging from the anatomical work of Alexandrowicz ('32, '32a, '34), the physiological studies of Yung (1878, 1879), and the anatomico-physiological papers of Jolyet & Viallanes (1892), Conant & Clarke (1896), and Bottazzi ('01). Stimulation of an augmentor nerve causes, as in *Limulus,* a stoppage of the heart beat in diastole; of an augmentor nerve, produces an increase in the heart rate and amplitude of *Palinurus* (Carlson, '05–'06a) and in the heart rate and tonus, but not amplitude, of *Maia* (Bottazzi, *loc. cit.*). In the crab, *Callinectes hastatus* (Conant & Clarke), there is, however, no evidence of tonic activity from either type of nerve. Thus, the thoracic ganglion complex can be removed without producing any apparent effect on the heart rate.

Lemoine (1868) once figured and described a median cardiac nerve issuing from the stomatogastric ganglion of the crayfish. Yung (1878, 1879) and Plateau (1880) stated that the existence of the nerve is incontestible; that it is an augmentor; and that cutting it produces a slowing of the heart rate. They were backed up by Mocquart (1883) in the shrimp and by Keim ('15) in the crayfish. On the other hand, Jolyet & Viallanes, Retzius (1890), Conant & Clarke, and Carlson ('04–'05, '08b) searched vainly for Lemoine's unpaired ''nerve cardiaque'' since stimulation and cutting in the region in which it was supposed to exist produced no apparent effects on the heart.

Other nerves from the thoracic complex innervate the valves and dorsal diaphragm (Alexandrowicz, '32, '32a, '34). The nerve fibers to the valves probably maintain the muscles of the latter in a state of contraction during the diastolic phase.

f. *Hexapoda.* The only detailed studies on the innervation of the heart of insects are those of Zawarzin ('11) on the larva of a dragonfly, *Aeschna;* of Alexandrowicz ('26) on the cockroach, *Periplaneta;* and of Opoczyńska-Sembratova ('36) on the phasmid, *Carausius morosus.* In these insects, as in *Limulus* and many Crustacea, there are no ganglion cells scattered about the walls of the heart. On either side of the heart of *Aeschna* is a longitudinal nerve which Zawarzin considered to be probably derived from the stomatogastric ganglion. Lyonnet (1760), in an exquisite anatomical work, noted that each side of the heart of a caterpillar receives a nerve from the homolateral stomatogastric ganglion. Each cardiac nerve of *Anax* (Maluf, '35) and *Aeschna* is but an elongated axon with no ganglion cells in the region of the heart but with neurilemma nuclei sparsely scattered. The heart also receives motor branches from the abdominal ganglia (*cf.* also Lyonnet, 1760). The cockroach and phasmid heart is provided with lateral nerves consisting chiefly of processes from ganglionic cells scattered alongside the nerve. Those of the cockroach, at least, are connected anteriorly with the stomatogastric ganglia.

Mechanical stimulation of the brain of a grasshopper, *Dictyphorus reticulatus* (Carlson, '05–'06a), frequently caused a cessation of the heart beat in a state of diastole. On the other hand, electrical stimulation of the brain of this grasshopper and of a moth, *Telea polyphemus,* often produced an augmentation in the rate and amplitude of the heart beat. The same augmentor effects occurred after severing all nervous connections of the brain except those connecting it with the thoracic and abdominal ganglia. The rate and amplitude of the heart beat were similarly augmented on stimulating the thoracic and abdominal ganglia. Electrical stimulation of the brain of a stag-beetle larva (Lasch, '12–'13), produced a retardation of the heart beat. It is evident that the inhibitor nerves are connected with the brain by way of the stomatogastric nervous system and are probably the lateral intrinsic nerves of the heart. The augmentor nerves are extrinsic nerves and issue from the abdominal ganglia.

Removal of the head has no effect on the periodic reversal of the heart beat of insects (Gerould, '33).

3. *Origin of the heart beat.*—a. *The myogenic basis of the beat.* The embryonic heart of *Limulus* (Carlson & Meek, '08) begins to

beat before any fundament of the cardiac nervous system has appeared. The heart of the lobster (Herrick, '09) begins to beat when the nervous system is only roughly blocked out and long before any nerves are developed. The heart of the larva of the dragonfly, *Anax junius* (Maluf, '35), will continue to beat rhythmically without any connections with ganglion cells. The excised heart of *Bombyx mori* (Kuwana, '32) will continue to beat even though the heart has no intrinsic ganglion cells. The same is probably true of *Corethra* larvae (Walling, '08) notwithstanding Dogiel's (1877a) assertion of "birnförmige Körper" in the heart of the latter. The heart beat of vertebrate embryos has been proved beyond doubt to be myogenic (His, 1893; Hooker, '11; Burrows, '12). Meager indirect evidence indicates that the heart of the crayfish (Plateau, 1879) is myogenic. About 0.5 mg. of curare were injected into the hæmolymph. At the end of an hour the animal appeared dead and was irresponsive to stimuli but the heart continued to beat for several hours. Among vertebrates, the classic experiments of Claude Bernard have shown that curare prevents transmission from nerve to muscle. One cannot say, however, whether the drug penetrated the neurilemma sheath, especially in view of other negative results on the effects of curare on arthropod hearts (p. 269).

b. *The neurogenic basis of the beat.* Owing to the presence of ganglion cells scattered about the heart wall of vertebrates after a certain stage of embryonic development, and owing to the fact that the vertebrate heart will continue to beat even after being detached from the rest of the nervous system, it has never been possible to determine whether the pulsations of the vertebrate heart are due to possible rhythmic impulses discharged from the intrinsic ganglion cells. Taking advantage of the condition in *Limulus,* Carlson ('04–'05a, '05–'06, '06) found that removal of the cardiac ganglion produces immediate and perpetual cessation of the beat (see also Garrey, '30) and that coördination is entirely dependent upon the integrity of the cardiac ganglion and lateral cardiac nerves. Carlson's classical experiments on coördination have been confirmed on an isopod (Alexandrowicz, '32b), on scorpions (Rijlant, '33a), and on *Limulus* (Nukada, '18; Dubuisson, '30–31a; Heinbecker, '33, '36). But Hoshino ('25), Dubuisson ('29, '30), and Heinbecker (*loc. cit.*) showed that the completely deganglionated heart of *Limulus* will continue to beat, after a temporary arrest, provided it is adequately distended. In the deganglionated heart the propagation of the contraction wave is slow, and not practically simultaneous throughout the length of the heart, as it is when the intrinsic nervous system is intact. These investigators thus concluded that the heart of even the adult *Limulus* is capable of myogenic automatism and Dubuisson ('30–'31, '31) considered that, even in the normal heart, the intrinsic nervous system is of importance solely in synchronizing the beat throughout the length of the heart. Heinbecker ('31, '33, '36) and Rijlant ('31c, d) showed that ganglion cell activity precedes muscular activity by 30–80σ. Rijlant ('31) presented more evidence for the neurogenic theory as applied to the normal *Limulus* heart by finding that the spontaneous discharges from the isolated cardiac ganglion correspond with the waves of the muscular action current. There were short waves superimposed on long waves (see also Hoffmann, '11, for the whole heart of decapods and *Limulus*), the superimposed waves being considered to represent associations.

Electrical stimulation of one of the lateral cardiac nerves of *Limulus* (Garrey, '33) caused the beats of the homolateral side to be superposed on a raised tetanic base while those on the opposite side of the heart were altered to a far lesser extent. This was held to show that the stimulated nerve does not innervate all of the contractile elements of the same side as would be the case if muscular conduction were effective. "The proof is conclusive that there is no muscular conduction in the normal adult *Limulus* heart, and consequently there can be no myogenic rhythm." The results of Dubuisson and of Heinbecker show that such an attitude is extreme and the statement "to a far lesser extent" implies only a quantitative difference between the rate of transmission in nerve and muscle. The heart muscle of arthropods is essentially a syncytium (see, for instance, Weismann, 1874; Gerschler, '10; Zawarzin, '11; Baumann, '21) and there is, hence, no apparent reason why muscular conduction cannot occur. From what has been said, there seems to be little ground for doubt, nevertheless, that the beat of the adult *Limulus* innervated heart is neurogenic.

The variations in temperature, affecting the ganglion cells alone, yield temperature coefficients which are almost identical with those for the whole heart (Garrey, '20, '20a).

The data of Magnus ('02) and Sollmann ('05–'06) indicate that the heart beat of an adult vertebrate is neurogenic, although Magnus failed to realize the implications of his results. "If the mammalian heart rhythm is myogenic, it is difficult to explain why pressure in the ventricular cavities is not just as efficient or even more efficient a stimulus to rhythm than the pressure in the coronary vessels. On the neurogenic theory afferent fibers or nerve endings in the walls of the coronary vessels are stimulated by the distension of the walls . . . " (Carlson, '06).

4. *Pacemakers and the sequence of the heart beat.* In 1669 Malpighi recorded a periodic reversal in the direction of the heart conduction of the silkmoth (*Bombyx*) pupæ and adults. Cornalia (1856) confirmed, on the pupa, Malpighi's observations. De Réaumur (1734) stated that in the *Bombyx* pupa and adult the pulsations are backward and, in the larva, forward. Bataillon (1893) confirmed this and noted that at the onset of metamorphosis, the time interval occupied by the backward pulsations gradually becomes predominant until, in the pupa, forward pulsations cease to occur. The truth, as Fischer ('18), Gerould ('29, '31), and Tirelli ('36) have observed, lies in a fusion of the findings of all three above investigators. Thus, while predominant, the backward pulsation is not the sole type of sequence in the pupa and the forward pulsation not the sole type in the adult. Reversals occur in the pupæ and adults of all Lepidoptera examined, in certian flies and beetles, and in hymenopterous adults. The alternations are fairly regular (Gerould, *loc. cit.* and '33). In lepidopterous larvæ the pulsations were always forward. No reversals have been noted in neuropterous odonate, or *Belostoma* adults (Gerould, '33; Maluf, '35), nor in dragonfly larvæ (Maluf, *loc. cit.*). Reversals occur in certain Crustacea (Leydig, 1889) and in unhealthy *Lumulus* adults (Pond, '20–'21). Jahn, Crescitelli, & Taylor ('36) found, in the grasshopper, that potential variation as well as direction of waves of contraction show reversals.

While in the healthy *Limulus* the pacemaker does not shift from end to end of the heart it varies in its location from time to time

(Garrey, '30; Dubuisson, '30–'31, '30–'31a) its only approximation to constancy being that the anterior segments normally beat later than the middle segments (Nukada, '18; Edwards, '20; Pond, '20–'21). The greater automatism of the fifth, sixth, and seventh segments is due to the fact that these segments have the greatest number of ganglion cells (Carlson, '04–'05b). The time sequence cannot be detected by the naked eye but when the heart is exhausted it is noticeable that the beat starts somewhere between the middle and posterior end (Carlson, '04–'05a). This is also generally true of the higher Crustacea (Plateau, 1880).

Heat, applied to local spots of the cardiac ganglion of *Limulus* (Garrey, '30), transfers the pacemaker to such spots and accelerates the heart beat. On the other hand, when localized cold is applied, "as long as any part of the ganglion remains at the original temperature . . . the original temperature will determine the rate of the whole heart. Even if three-fourths of the ganglion is thus cooled there is no change in rate."

Considerable light has been thrown, on certain conditions producing reversals, by Yokoyama ('27) and Gerould ('31) who found that premature reversal of the beat in *Bombyx* can be induced in the larva about to spin by sealing the posterior-most pair of spiracles. Injection of lactic acid in the posterior region of the abdomen or narcotizing this region with ether, alcohol, or xylol acted similarly. The fact, that when the metabolic rate of the posterior end is lowered the next predominant region becomes the anterior end, indicates that the direction of the heart beat depends upon a U-shaped excitability gradient in the heart, generally with the highest point at the posterior end and the next highest at the anterior end. When the high point, or pace-maker, at one end is demolished the other acquires the lead. In this connection it is noteworthy that Gerould ('33) found that the frequency of the beats in a given direction gradually decreases until a reversal occurs.

The pulsatile organs in the legs of Hemiptera (Locy, 1884) undergo contraction from the distal to the proximal end.

It has been noted above that the rate of propagation of the contraction wave varies with factors such as fatigue and stretch. To such should be added temperature. In the *Limulus* heart, under ordinary experimental conditions, the rate of propagation has been found to be about 73 cm. per second (Edwards, '20; Pond, '20–'21). Carlson's ('05–'06) data show that the rate of conduction in the cardiac ganglion is of the same magnitude, namely, ca. 41 cm. per second, this being about 9 times less than that in the motor nerves to the limbs. He also produced evidence ('05–'06b) for a direct relation between the rate of conduction in a motor nerve and the rapidity of contraction in the muscle it innervates. But Dubuisson ('30–'31) found that the speed of the contractile wave of the *Limulus* heart, when healthy and adequate distended, is generally over 1,000 cm. per second although quite variable. This is much higher than any of the values given above and requires confirmation. The rate of propagation of the contraction wave of the lobster's heart (Clarke, '27) is 40 cm. per second and, as in *Limulus,* the sequence cannot be detected by the naked eye.

The sequence of the heart beat in insects is much lower than in *Limulus* and the higher Crustacea and is thus easily detected by the unaided eye. The maximal, average, and minimal rates of conduction of the contraction wave in the larva of the stag-beetle, *Lucanus cervus* (Lasch, '12–'13), are 44.3, 27.2, and 19.5 cm. per second; in the heart of the moth larva, *Cossus cossus* (A. Seliškar, unpublished; *cf.* Clark, '27), the conduction rate is about 2.4 cm. per second at 15° C.

5. *Frequency.* The heart rate varies with numerous factors such as general metabolic rate, fatigue, stretch, and the presence of various agents in the blood. Even under apparently identical conditions the heart rate of different individuals of a given species and age varies considerably (Table I). In a given individual under normal conditions, however, the rate is fairly constant (Pickering, 1894; Robertson, '06; Maluf, '37) although the frequency of the periodic arrests which occur in certain species is very variable. While there is no well defined relationship between the heart rate and the phylogenetic position, it is clear that the rate in Crustacea, Scorpionidæ, and Pycnogonida is considerably higher than among *Limulus* and insects. This is correlated with the fact that only few insects have blood gills, and even when these exist they are of no marked respiratory significance (Fox, '21). Exception should be made of *Chironomus* larvæ, which

have a high heart rate and *the blood of which has a significant respiratory function* (Leitch, '16).

Even before van 't Hoff and Arrhenius made their classical quantitative studies on the relationships of the rate of chemical reactions to temperature, Carus (1824) and Newport (1839) found that warmth accelerates the heart rate of crustaceans and insects. In the crustacean, *Ceriodaphnia* (Robertson, '06), between 15° and 31° C., the Q_{10} averages 2.03, varying between 1.14 and 2.66 and falling with rise in temperature. Between 8° and 28° the Q_{10} for crayfish embryos is 2 to 2.6 (Zehnder, '34). In the insects and crayfish studied by Polimanti (Table I) the Q_{10} is never as high and varies between 1.2 and 1.6, falling with rise in temperature. Both the Q_{10} and μ of enzymatic processes *in vitro* decrease regularly with temperature possibly due to a decrease in the viscosity of the substratum (Bělehrádek, '28, '30) although Stiles ('30) has concluded that viscosity plays only a small rôle in determining the rate of biological reactions. For interpretations of Crozier's temperature characteristics for the heart rate of arthropods *cf.* Crozier & Federighi ('25), Fries ('26), Crozier & Stier ('27, '27a), Matsuki ('27), Henderson ('27), Koidsumi ('28, '31), Stier & Wolf ('32), and Barnes ('37).

Moderate temperatures, such as 35° C., are lethal to a number of Crustacea (Robertson, '06; Coker, '34, '34a; Maluf, '37a). The optimum temperature for the rate and amplitude of the *Limulus* heart is 10°–15° C. (Carlson, '05–'06c) and the upper and lower limits for a heart in good condition are −1° and 42° C. When in poor condition the heart muscle may cease to respond at 25°. The cardiac ganglion and the intrinsic motor fibers are more heat-resistant than the heart muscle.

Polimanti ('15a) presented evidence that the heart rate of silkmoth larvæ decreases with decreasing light wave-length in the visible region. It was not, however, determined whether blinded animals will react likewise or whether the effect is merely one of intensity or of the *quantity of energy absorbed.* The italicized factor has been overlooked in all studies on the photoreception of animals. Ultra-violet rays soon bring the heart of daphnids to a standstill (Tchakhotine, '35).

The substance released by the eye-stalks of many Crustacea and which produces a condensation of the pigment granules in the

TABLE I
A REPRESENTATIVE LIST

Species	Average heart rate per min. at 25° C.[1]	Remarks	Investigators
Xiphosura:			
Limulus	12–28	....	Carlson ('04–'05a) Dubuisson ('30–'31)
Scorpionideæ	120–225	Greater rate in young of a given species.	Rijlant ('33, '33a)
Acarina	90–300	....	“
Pycnogonida:			
Polixichilidium	180–370	....	“
Crustacea:			
Ceriodaphnia	6	....	Robertson ('06)
Daphnia	312	....	Pickering (1894)
Daphnia	188–289	....	Knoll (1893)
Cancer	9–120	....	Carlson ('06)
Cancer	15–30	When bled.	“
C. pagurus	80.5	....	Eckhard (1867)
Pagurus longicarpus	167–250	Rate greater in young.	Maluf ('37)
Carcinus maenas	16.8–94.5	....	Plateau (1880)
Maia squinado	37	....	Knoll
M. verrucosa	98	....	Polimanti ('13)
Mysis	380	....	Knoll
Caprella	180–240	....	“
Squilla eusebia (larvæ)	216	....	“
Porcellana (zœa)	255	....	“
Astacus fluviatilis	119–153	....	Plateau
A. fluviatilis	57	....	Polimanti
Cambarus virilis	59	....	Welsh ('37)
C. virilis	82	Injected with eye-stalk.	“
Hippolyte	360	Pale or nocturnal phase.	Keeble & Gamble ('00)
Hippolyte	225	Dark or day phase.	“ “
Insects:			
Oryctes nasicornis	18	Exposed heart.	Polimanti
Bombyx mori (larvæ)	54	....	Polimanti ('15)
Lucanus cervus (larvæ)	24	....	Lasch ('12–'13)
Chironomus dorsalis *C. plumosus* (larvæ)	162	....	Dubuisson ('29)

---

[1] A Q_{10} of 2 is assumed. "Room" temperature is taken as 20° or 25° C., depending upon the locality or season.

chromatophores also raises the heart frequency (Welsh, '37). In 1900, Keeble & Gamble, too, had noted that the pale phase of a prawn is accompanied by a higher heart rate than the dark phase. They, however, supposed such to be under the entire control of the nervous system.

The heart rate is not necessarily a strict index of the metabolic rate, for, while small hermit crabs (Maluf, '37) have a significantly higher heart rate than the larger individuals (see also Rijlant, '33, '33a for scorpions), their rate of oxygen consumption is not appreciably greater. Furthermore, while the heart rate of Crustacea is generally greater than that of insects (see table I) the metabolic rate of the latter is commonly much higher (*cf.* Parhon, '09). This is an outcome of the fact that the circulation has ceased to be of respiratory importance to most insects.

6. *Refractoriness, tetanus, and automatism.* It is generally known that, because of the presence of a relatively long refractory period (occurring during systole), the fundamental contractions of the vertebrate heart cannot be summated and tetanus cannot be produced. By stimulation at a low frequency, however, summation of the underlying contractions of the vertebrate heart is possible. The tetanus then is not the result of a fusion of the fundamental contractions (which does not occur) but of the tonus contractions with partial or even complete masking of the fundamental contractions (see Ranvier, 1880; Langendorff, 1895; Walther, 1898; Cyon, '00; Danilewsky, '05; especially Porter, '05–'06, and several others).

According to some investigators the heart of all arthropods and of all invertebrates, so far as studied, has no refractory period though there is, during systole, a condition of reduced excitability (Hunt, Bookman, & Tierney, 1897, for the lobster; Carlson, '03, for tunicates, molluscs, and crustaceans; Carlson, '06a, '06b, '07, '08a, for *Limulus*; Hoffmann, '12, for *Maia*). That the heart of invertebrates can, in most cases,[2] be tetanized was first noted by Eduard and Ernst Weber (1846), the classical "Weber brothers" often mentioned in physiological text-books; and has been confirmed by the above investigators as well as by Brandt (1865), Plateau (1878, 1880), Dogiel (1894), Polimanti ('13), de Boer

---

[2] The heart of certain gastropods (Carlson, '03) cannot be tetanized.

('28), and Garrey ('33). Hunt, Bookman, & Tierney pointed out that *the tetanic contraction is due to the summation of single fundamental contractions* and is not a prolonged single contraction.

Recently, de Boer ('28) and Izquierdo ('31), both of which testified to the capacity of the crab's heart to undergo tetanus, found that the heart of *Maia* does undergo total refractoriness of short duration (0.2 sec.) during systole. They claim that Hoffmann's results were obtained on an empty heart and that Carlson's results are due to an error in technique since the point of stimulation should be close to where the lever of the kymograph is attached. On *a priori* reasons one would expect a refractory period to occur in any automatic tissue and, since vertebrate skeletal muscle has a short refractory period (0.0015 sec.) and can be tetanized, there is no reason why the same should not apply to the invertebrate heart.

For many years there has existed the opinion that there is an immediate causal connection between automaticity and refractoriness, the latter state being conceived as one of "charge." This has recently been supported in a stimulating speculative article by Ritchie ('32). For the following reasons such an attitude should not be allowed to pass without challenge: 1. "In the same heart the parts possessing the greatest degree of automatism may exhibit a lesser degree of refractory state than the part of the heart not automatic," *e.g.,* the mud turtle (Carlson, '07). 2. "Refractoriness is exhibited by certain tissues that are not automatic under normal conditions," *e.g.,* the turtle ventricle (Carlson, '07). 3. "The motor nerve fibers to the frog's skeletal muscles exhibit a refractory period of 2/1,000 second; while some of the motor cells in the spinal cord of the frog show a refractory period of from 1/10 to 1/20 second. Yet these nerve cells exhibit no greater automatism than the motor nerve fibers. 4. Some of the pyramidal cells of the mammalian cerebral cortex exhibit refractory periods as long as 1/12 to 1/15 second. Yet these cells are not active automatically, at least as far as their motor functions are concerned" (Carlson, '06a).

7. *The all-or-nothing rule.* Hunt, Bookman, & Tierney (1897) considered that this rule is not applicable to the lobster's heart,

as it is, for instance to the frog and mammalian heart, since increase of stimulus increased the amplitude of the contraction or tetanus. Carlson ('03) held to such a view but later ('06b) noted that "the pulsating or quiescent heart (of Crustacea and Mollusca) *whose excitability and conductivity are but slightly impaired* [italics mine] responds by a contraction of uniform strength to stimuli of increasing intensity within a wide range, but an increase of intensity above this range is followed by beats of increased strength. . . ." Nothing in the above is serious evidence against the applicability of the all-or-nothing rule to the arthropod heart, but the results of Garrey & Knowlton ('34–35) on *Limulus* appear to be damaging. They obtained a summation of repetitive stimuli which yielded an augmentation of amplitude but not of frequency. The effects were shown to be purely motor and not afferent. Given a muscle area innervated by two different motor nerve fibers; when any one of these nerves is subliminally stimulated no augmentation is elicited but "we must still admit that the nerves are transmitting effects to the muscle otherwise it is difficult to explain the fact that stimulation of another nerve provokes an augmented effect." Even if one takes for granted that the heart muscle of *Limulus* is a syncytium, the results of the above investigators do not appear to be difficult to harmonize with the all-or-nothing rule. Thus, in his study on single with microelectrodes, *Gelfan* ('31, and elsewhere) was able to obtain localized contractions. These, however, are not accompanied by an electrical action potential, as is generally true for the all-or-none effects (Gelfan & Bishop, '32). It has, therefore, come to be accepted that the all-or-nothing rule is characteristic of the excitation process as distinct from the contractile one.

8. *Effects of various external agents.* a. *Perfusion liquids.* Modifications of Ringer's solution have been described for the intact heart of *Daphnia* (Lévy, '27), excised heart of *Astacus fluviatilis* (Dohrn, 1866, and Lévy, '33), *Cambarus clarkii* (Lindeman, '28), *Maia* and *Homarus* (Hogben, '25), and *Palinurus alandii* (Zoond & Slome, '28). Ordinary sea water is a fair perfusion medium for the hearts of poikilosmotic marine forms (Polimanti, '13; Fredericq, '22; Hogben, '25; Macallum, '26; Carlson, and others). Basing their figures on careful analysis of the blood

of the American lobster, Cole, Kazalski, & McComas ('38) adopted the following solution as best fitting the lobster heart: NaCl, 0.452; KCl, 0.015; $CaCl_2$, 0.025; $MgCl_2$, 0.004; $MgSO_4$, 0.004 (all in moles). Small amounts of NaOH were added to bring the pH to 7.4. With this solution the intact heart could maintain its vigor for 36 hours. Van't Hoff's solution and sea water were found to be poor perfusing media. With the former the heart could beat for about 1 hour; and with the latter up to 4 hours. All ideal perfusion media should be made up according to accurate analysis of the blood of the animal in question.

The intact heart of the stick insect, *Carausius,* and of the moth larva, *Cossus cossus* (A. Seliškar, unpublished, *cf.* Clark, '27), "beat well when irrigated with a fluid of the following molar composition: NaCl 0.22, KCl 0.002, $CaCl_2$ 0.001. Removal of Ca arrested the hearts in a few minutes, but removal of KCl produced no visible effects in 2 hours. Increase of KCl to 0.02 molar produced slowing of the rate of conduction . . . and arrested it in a few minutes. . . . Reduction of NaCl to 0.11 molar reduced the frequency of the heart. . . . The presence of K seems much less important for arthropod than for vertebrate hearts, and in many cases the heart functions normally in its absence. . . . Excess of K produces arrest." The reason these results have been quoted in full is because they are remarkable in view of the fact that the blood of insects is rich in potassium and contains sodium in relatively small amounts (Bishop, Briggs, & Ronzoni, '25; Brecher, '29; Drilhon, '34). It is, however, probable that the K is mainly present as unionized K urate.

b. *Various cations.*—(i) *Sodium, potassium, lithium, rubidium.* In isotonic NaCl the heart of the crawfish, *Palinurus* (Fredericq, '22; Zoond & Slome, '28) enters systolic arrest. One per cent and 2 per cent NaCl added to Lindeman's ('28) Ringer modification causes a marked increase in the rate and amplitude but a decrease in tonus of the contractions of the heart of *Cambarus clarkii.* Carlson ('06–'07, '08), whose results have shown that the deganglionated unhealthy heart of *Limulus* will not pulsate automatically, found that such a heart (like curarized vertebrate skeletal muscle, see the classic work of Loeb, 1899) twitches rhythmically in pure NaCl and that the rhythm may closely approach the normal rhythm. If placed in normal sea water or plasma, after development of the "idio-muscular" rhythm, the contractions are quickly abolished. He suggested that NaCl may alter muscular tissue so as to make conductivity from cell to cell possible. Such a conclusion is no longer likely since we know that the healthy deganglionated heart, when adequately stretched, will pulsate rhythmically. It is possible that the effects of NaCl are not qualitative but solely quantitative, *i.e., enhance* the conductivity from cell to cell.

Eventually pure NaCl brings the heart of *Limulus* and *Homarus* (Cole, *et al.*) to a systolic standstill. An analysis of the electrocardiogram, during the process of NaCl arrest has been made by Hoffmann ('11a).

Potassium, as 0.6 N KCl, is a primary stimulant (frequency and tonus) of the cardiac ganglion of *Limulus* (Carlson, '06e) but has opposite effects on a heart from which the ganglion had been removed. The same applies to rubidium. Lithium is a primary stimulant of the heart of the crayfish (Lindeman, '28) and is capable of only partially replacing sodium in a suitable Ringer's solution. Pure KCl, in the same concentration as in sea water, causes a primary decrease in frequency but an increase in amplitude of the heart of *Maia* (Polimanti, '13). The same is, however, also true for $MgCl_2$ (group II of the periodic table). It is the excess K in hypertonic Ringer's that produces a decrease in frequency and increase in amplitude of the heart beat of the crayfish (Cardot, '21, '22). Hogben ('25) noted that excess K, Na, or Rd first excites and then depresses the heart beat of *Maia* and *Homarua,* and that the eventual arrest is in diastole. Cæsium had no very marked effects. It is evident that ions belonging to group I of the periodic table (monovalent), when in isotonic solution, are primary stimulants.

(ii) *Calcium, magnesium, strontium, and barium.* An excess of Ca, Mg, or Sr causes a stoppage of the *Palinurus* heart in diastole; but Mg cannot be successfully substituted for Ca in the perfusion liquid (Zoond & Slome). Ringer's solution containing about 10 times the ordinary amount of Ca results in a decline in tonus and resultant swelling of the heart of *Daphnia* (Lévy, '27). Pure 0.6 N $CaCl_2$, $SrCl_2$, or $MgCl_2$ depresses the action of the median dorsal cardiac ganglion and heart muscle of *Limulus* (Carlson, '06e) without any indications of primary stimulation. $BaCl_2$, on the contrary, is an intense primary stimulant of both.

The addition of 0.028 per cent $SrCl_2$ or $BaCl_2$ to the Ringer's solution for the perfusion of crayfish hearts (Lindeman, '28) causes an increase in tonus followed by an arrest in systole; but substituting 0.020 per cent $SrCl_2$ for the 0.024 per cent $CaCl_2$ in the usual perfusion solution results in maintaining the normal rhythm for five hours. Ca is a primary inhibitor of the heart of *Maia* (Polimanti, '13) and produces diastolic standstill (Hogben, '25).

Since a pure isotonic solution of Ca cations tends to produce cessation of the heart beat in diastole and a pure isotonic solution of Na ions cessation in systole, these two ions act antagonistically when together in solution. It is, therefore, not surprising that Zoond & Slome (*loc. cit.*) maintained rhythmic contractions of the heart of *Palinurus* in a solution containing only Na and Ca cations. Na and Ca also act antagonistically in their action on the cardiac ganglia, the former producing primary stimulation and the latter primary depression. The cations in both groups of the periodic table, as can be noted from what has been said, do not *all* act in accordance with their classification in the table. It may be said, however, that the monovalent metals antagonize the effects of the bivalent metals and that Na and K tend to stimulate nervous and muscular cells to activity while Ca, Mg, and Sr tend to depress activity. In fact, Loeb ('06) suggested that the periodic cessation of irritability in nerve or muscle, giving rise to rhythmic action, is due to the periodic substitution of Ca or Mg ions for Na or K ions, the ions passing alternately from the interior of the cell to the surface.

c. *Non-electrolytes.*—(i) *Urea, glycerin, and sucrose* have a primary stimulating action on the cardiac ganglion of *Limulus* (Carlson, '06e). The pulsations of the heart of *Palinurus* (Fredericq, '22) cease rapidly when the perfusion medium is sea water containing 2 per cent urea. In complete contrast, the heart of the dogfish (*cf.* Clark, '27) imperatively requires urea if it is to function normally. A vigorous cardiac ganglion of *Limulus,* inactivated by a pure isotonic solution of sucrose and again restored by

Limulus blood plasma or sea water, will, on a second bath in a sugar solution, come to rest in a much shorter time. The same results are produced by pure isotonic solutions of urea and glycerin. Carlson ('06d) hence stated that the theory which holds that the heart standstill is due to outward diffusion and dilution of the electrolytes about the cells (see Loeb above) fails to explain these facts for there apparently must be as many of them, qualitatively and quantitatively, during the restored rhythm as during the original if the heart pulsations are due to the presence of a definite quantity and ratio of electrolytes in the automatic tissue. A pure isotonic solution of sucrose may, however, have damaged the heart in some irreversible way.

(ii) *Adrenalin and thyroid extract,* in unstated concentrations, increase the heart rate of *Daphnia* (Hykes, '26). In a 1:100,000 conc. adrenalin may cause a slowing of the rate; in a 1:10,000 concentration, it may cause an acceleration both of the isolated and intact heart of *Daphnia* (Lévy, '27). It has a primary stimulating effect on the heart ganglion and heart beat of *Limulus* (Carlson, '06f, and Heinbecker, '36) and increases the frequency and tone of the heart of *Maia* (Hogben & Hobson, '23–'24).

(iii) *Pituitary and thymus extracts* slow the heart rate of *Daphnia* (Hykes, *loc. cit.*) but, in quantities comparable to those which exist in the mammalian uterus, pituitary extract has no apparent action on the excised heart of *Maia* (Hogben & Hobson, '23–'24).

(iv) *Anaesthetics* (ether, chloroform, chloretone, chloral hydrate, and ethyl alcohol) have, in weak concentration, a primary stimulating action on the cardiac ganglion of *Limulus* (Carlson, '06) and chloroform initially increases solely the amplitude of the cardiac beat of the lobster (Plateau, 1880). Chloral hydrate at once slows the heart rate of *Daphnia* (Lévy, '27) but raises the tonus slightly.

(v) *Alkaloids.* Strychnin, caffein, curare, nicotin, atropin, cocain, pilocarpin, physostigmin, aconitrin, veratrin, saponin, quinin, digitalin, adrenalin, and ergot have, in weak concentration, a primary stimulating effect on the cardiac ganglion of *Limulus* (Carlson, '06f, '22, and Heinbecker, '36). They paralyze or block the cardio-inhibitor nerves but not the cardio-augmentor nerves (Carlson, '22). The paralysis of the heart tissues that ensues occurs in the following order: ganglion, motor plexus, muscle (Meek, '08). Acetylcholin (1–500) has a primary depressant action and will cause a cessation of spontaneous activity in 15 minutes (Heinbecker, *loc. cit.*).

Nicotin, applied to the heart of the roach or of larvæ of the moth *Prodenia eridamia* (Yeager & Gahan, '37), in concentrations varying from 0.0005 to 10 per cent by weight, "causes initial stimulation followed by partial depression at relatively intermediate concentrations and stimulation followed by complete depression and paralysis at relatively high concentrations." The effects were generally reversible. Nicotin is known to decrease the ability of striated muscle to recover from the contracted state and thus evokes systolic arrest of the insect heart (Yeager, '38).

Even in large doses, curare did not paralyze cockroaches or beetles (Moseley, 1871) and, in Crustacea, the action of curare is reputedly slower than it is among vertebrates (Yung, 1878, Plateau, 1879, 1880; Lapicque & Lapicque, '10, '36).

Digitalin, atropin, caffein, veratrin, and nicotin, in weak concentration, have a primary stimulating action on the heart of Crustacea (Yung, 1878; Pickering, 1878; Plateau, 1880) but muscarin, theobromin, and xanthin have no apparent effects on the heart of *Daphnia* (Pickering, *loc. cit.*).

d. *Hydrogen ions.* The arthropod heart can function normally within a relatively wide pH range. The optimum pH for the excised heart of *Palinurus* (Zoond & Slome, '28) in a balanced solution of only Na and Ca chlorids is 5.0. On the alkalin side it loses tone at about pH 8.0 but is not tolerant of slightly greater acidity than pH 5.0. The rhythm of the excised heart of a crayfish has been stated to be normal within the pH range of 5.5 to 9.0 in Lindeman's ('28) perfusion medium. At pH's a little below 5.5 there was an increase in tone but a decrease in the amplitude and frequency. Six-tenths N HCl has a primary stimulating effect on the cardiac ganglion and a primary depressant action on the heart muscle of *Limulus* (Carlson, '06c). Six-tenths N KOH has a primary stimulating effect on both the heart muscle and cardiac ganglion of *Limulus.* At pH 3 there is a marked decrease in the frequency of the heart of trichopterous larvæ. The effects are reversible if not prolonged (Krey, '37).

e. *Carbon dioxid* poisoning causes diastolic standstill of the heart of *Limulus* (Newman, '06). If the condition is not prolonged recovery is rapid. The heart muscle is less sensitive than the cardiac ganglion.

f. *Oxygen lack.* The cardiac ganglion of *Limulus* (Newman, *loc. cit.*) will retain its activity unimpaired, when in a very deficient oxygen supply, for several hours. Lowering the oxygen pressure of the perfusion medium decreases the heart rate in the decapods (Plateau, 1880).

SUMMARY

1. The circulatory system of arthropods is of the open type. This means that the aorta and arteries, when the latter are present, open into the hæmocœle. Most arthropods have no veins, or sinuses, but some Crustacea (*e.g.,* amphipods and læmodipods) do have veins though no arteries other than the dorsal aorta. The veins open distally into the hæmocœle and communicate proximally with the pericardial sinus.

2. Blood is aspirated into the pericardial sinus during the diastolic phase of the heart beat. The alary muscles of the dorsal diaphragm, by stretching the heart muscle, augment this effect. The extra-arterial pressure in the limbs of arthropods is less than atmospheric.

3. The gills of the crab do not offer much resistance since they lower the blood pressure through only 6 mm. of water. In arthropods which respire by way of gills or lung-''books,'' the blood must pass through such directly before entering the heart. This implies that the heart is in the same transverse region of the body as the gills or lung-''books'' (*e.g.,* in the thorax in amphipods and in the abdomen in stomatopods). In those whose blood has no significant respiratory function the heart is located in the same transverse region of the body as that of the food-absorptive portion of the gut (*e.g.,* the abdomen in insects).

4. Since circulation is of the open type, movements of the viscera and skeletal muscles greatly enhance the circulation.

5. The heart of many arthropods (*Peripatus, Limulus,* scorpions, spiders, many crustaceans, and ''myriapods'') is supplied either with a median dorsal ganglion, or, as in cockroaches, with

a chain of ganglion cells on each lateral side. The heart of dragonfly larvæ is innervated solely by a pair of large lateral axons. The intrinsic cardiac ganglia receive nerve fibers from the central nervous system and give off efferent nerve fibers to the heart muscle and receive afferent fibers from such. The hearts of certain Crustacea, in contrast to those of *Limulus* and insects, contain ganglion cells scattered in their walls.

6. The heart of many arthropods has been shown to be supplied by inhibitor and augmentor fibers. In *Limulus,* at least, the action of these nerves is directly on the intrinsic cardiac ganglia.

7. The heart beat of adult *Limulus,* isopods, scorpions, and probably spiders is normally neurogenic. Myogenic automatism is, however, possible if the heart muscle is adequately distended.

8. The heart beat in *Limulus,* lobster, and vertebrate embryos is myogenic. So is the heart beat of dragonfly larvæ.

9. The pacemaker is usually at the posterior end of the heart. But there is a continuous shift and, in certain instances, reversals occur at regular intervals.

10. The tetanus of the heart muscle of arthropods is the result of a summation of several fundamental contractions. This is made possible by a not too long refractory period.

The writer wishes to thank Prof. T. Cunliffe Barnes for having read and criticized this article. All responsibility, however, rests with the former.

BIBLIOGRAPHY

AGASSIZ, L. 1851. Note sur la circulation des fluides chez les insectes. Ann. Sci. nat., 15(iii): 358.

ALEXANDROWICZ, J. S. 1912–13. Zur Kenntnis des sympathischen Nervensystems einiger Wirbellosen. Zs. allg. Physiol., 14: 358.

———. 1926. The innervation of the heart of the cockroach, *Periplaneta orientalis.* Jour. Comp. Neur., 41: 291.

———. 1932a. The innervation of the heart of the Crustacea. I. Decapods. Quart. Jour. Micr. Sci., 76: 511.

———. 1932b. Quelques expériences sur le fonctionnement du système nerveux du coeur des crustacés isopodes. C. r. Soc. Biol., 108: 1270.

———. 1934. The innervation of the heart of the Crustacea. II. Stomatopoda. Quart. Jour. Micr. Sci., 76: 511.

Asher, L., and Garrey, W. E. 1930. Some conditions affecting responses of Limulus heart to artificial and natural stimulation. Amer. Journ. Physiol. 94: 619.

Audouin, V., and Edwards, H. M. 1827. Recherches anatomiques et physiologiques sur la circulation dans les crustacés. I. Ann. Sci. nat., 11: 283.

———, and ———. 1827a. II. *Ibid.*, 11: 352.

Bataillon, E. 1893. La métamorphose du ver a soie et le déterminisme evolutif. Bull. sci. de la France et de la Belg., 25: 18.

Barnes, T. C. 1937. Textbook of general Physiology. Philadelphia, 544 pp.

Barratt, J. O. W., and Arnold, G. 1911. A study of the blood of certain Coleoptera: *Dytiscus marginalis* and *Hydrophilus piceus.* Quart. Jour. Micr. Sci., 56: 149.

Baumann, H. 1921. Das Gefäszsystem von *Astacus fluviatilis* (*Potamobius astacus* L.). Ein Beitrag zur Morphologie der Decapoden. Zs. wiss. Zool., 118: 246.

Behn, W. F. G. 1835. Découverte d'une circulation de fluide nutritif dans les pattes de plusieurs insectes hémiptères, circulation qui et independente des mouvements du vaisseau dorsal, et se trouve sous la dépendence d'un organe moteur particulier. Ann. Sci. nat., 2(iv): 5.

Bělehrádek, J. 1928. Le ralentissement des réactions biologiques par le froid est causé par une augmentation de la viscosité du protoplasme. Protoplasma, 3: 317.

———. 1930. Temperature coefficients in biology. Biol. Rev. 5: 30.

Berger, E. 1876. Über das Vorkommen von Ganglienzellen im Herzen vom Flusskrebses. Sitzber. d. math.-naturwiss. Classe d. kaiser. Akad. der Wissensch., Wien, 74 (i): 422.

Bergh, R. S. 1902. Beiträge zur vergleichenden Histologie. III. Über die Gefässwandung bei Arthropoden. Anat. Hefte, 19: 349.

Bervoets, R. 1913. Notes sur la circulation du sang dans les ailes des insectes. Ann. Soc. entom. Belg., 57: 184.

Bishop, G. H. 1923. Autolysis and insect metamorphosis. Jour. Biol. Chem., 58: 543.

———, Briggs, A. P., and Ronzoni, E. 1925. Body fluids of the honeybee larva. II. Chemical constituents of the blood and their osmotic effects. *Ibid.*, 66: 77.

de Boer, S. 1928. Vergleichende Physiologie des Herzens von Evertebraten. I. Untersuchungen bei *Maia verrucosa.* Zs. vergl. Physiol., 7: 445.

Bottazzi, P. 1901. Ueber die Innervation des Herzens von *Scyllium canicula* und *Maja squinado.* Zbl. f. Physiol., 14: 665.

———. 1902. Untersuchungen über das viscerale nervensystem der decapoden Crustaceen. II. Zs. f. Biol., 43: 341.

Brandt, A. 1865. Physiologische Beobachtungen am Herzen des Fluszkrebses. Bull. Acad. Sci. St. Petersb., 8: 422.

BRECHER, L. 1929. Die anorganischen Bestandteile des Schmetterlingspuppensblutes (*Sphynx pinastri, Pieris brassicae*). Veränderungen im Gehalt an anorganischen Bestandteilen bei der Verpuppung (*Pieris brassicæ*). Biochem. Zs., 211: 40.

BROCHER, F. 1916. Observations biologiques et physiologiques sur les dyticides. Arch. Zool. expér. génér., 55: 347.

———. 1920a. Étude expérimentale sur le fonctionnement du vaisseau dorsal et sur la circulation du sang chez les insectes. III. Le *Sphinx convolvuli. Ibid.,* 60: 1.

———. 1920b. Étude expérimentale sur le fonctionnement du vaisseau dorsal et sur la circulation du sang chez les insectes. Ann. Soc. entom. de France, 80: 209.

———. 1922. Étude expérimentale sur le fonctionnement du vaisseaux dorsal et sur la circulation du sang chez les insectes. V. La *Periplaneta orientalis. Ibid.,* 9i: 156.

VON BRÜCKE, E. T. 1925. Die Bewegung der Körpersäfte. (In H. Winterstein's Handbuch d. vergl. Physiol., vol. I, no. 1, pp. 882–947.)

———, AND SATAKE, J. 1912. Der arterielle Blutdruck des Hummers. Zs. allg. Physiol., 14: 28.

BURROWS, M. T. 1912. Rhythmical activity of isolated muscle cells *in vitro.* Sci., 36: 90.

CARDOT, H. 1921. Action des solutions de Ringer hypertoniques sur le coeur isole d'*Helix pomatia.* C. r. Soc. Biol., 85(ii): 813.

———. 1922. Reaction du coeur isolé de l'éscargot a une augmentation du taux du potassium. *Ibid.,* 87(ii): 1193.

CARLSON, A. J. 1903. The response of the hearts of certain molluscs, decapods and tunicates to electrical stimulation. Sci., 17: 548.

———. 1904–05. Comparative physiology of the invertebrate heart. Biol. Bull., 8: 123.

———. 1904–05a. The nervous origin of the heart-beat in *Limulus,* and the nervous nature of coordination or conduction in the heart. Amer. Jour. Physiol., 12: 67.

———. 1904–05b. Further evidence of the nervous origin of the heart-beat in *Limulus. Ibid.,* 12: 471.

———. 1905. The nature of cardiac inhibition with special reference to the heart of *Limulus. Ibid.,* 13: 217.

———. 1905–06. On the mechanism of co-ordination and conduction in the heart with special reference to the heart of *Limulus. Ibid.,* 15: 99.

———. 1905–06a. Comparative physiology of the invertebrate heart. IV. The physiology of the cardiac nerves in the arthropods. *Ibid.,* 15: 127.

———. 1905–06b. Further evidence of the direct relation between the rate of conduction in a motor nerve and the rapidity of contraction in the muscle. *Ibid.,* 15: 136.

———. 1905–06c. Temperature and heart activity with special reference to the heat standstill of the heart. *Ibid.,* 15: 207.

———. 1906. Comparative physiology of the invertebrate heart. V. The heart rhythm under normal and experimental conditions. *Ibid.*, 16: 47.

———. 1906a. Comparative physiology of the invertebrate heart. VI. The excitability of the heart during the different phases of the heart beat. *Ibid.*, 16: 67.

———. 1906b. Comparative physiology of the invertebrate heart. VII. The relation between the intensity of the stimulus and the magnitude of the contraction. *Ibid.*, 16: 85.

———. 1906c. Comparative physiology of the invertebrate heart. VIII. The inhibitory effects of the single induced shock. *Ibid.*, 16: 100.

———. 1906d. On the cause of the cessation of the rhythm of automatic tissues in isotonic solutions of non-electrolytes. Amer. Jour. Physiol., 16: 221.

———. 1906e. On the chemical conditions for the heart activity, with special reference to the heart of *Limulus*. *Ibid.*, 16: 378.

———. 1906f. On the point of action of drugs on the heart with special reference to the heart of *Limulus*. *Ibid.*, 17: 177.

———. 1906–07. The relation of the normal heart rhythm to the artificial rhythm produced by sodium chloride. *Ibid.*, 17: 478.

———. 1907. On the mechanism of the refractory period of the heart. *Ibid.*, 18: 71.

———. 1907a. On the mechanism of the stimulating action of tension on the heart. *Ibid.*, 18: 149.

———. 1908. The conductivity produced in the non-conducting myocardium of *Limulus* by sodium chloride in isotonic solution. *Ibid.*, 21: 11.

———. 1908a. A note on the refractory state of the non-automatic heart muscle of *Limulus*. *Ibid.*, 21: 19.

———. 1908b. Vergleichende Physiologie der Herznerven und der Herzganglien bei den Wirbellosen. Erg. der Physiol., 8: 371.

———. 1922. A note on the action of curare, atropine, and nicotine on the invertebrate heart. Jour. Gen. Physiol., 4: 559.

———, and Meek, W. J. 1908. On the mechanism of the embryonic heart rhythm of *Limulus*. Amer. Jour. Physiol., 21: I.

Carpenter, W. B. 1854. ''Principles of comparative physiology.'' Lond., 770 pp.

Carus, C. G. 1824. ''Von den äuszeren Lebensbedingungen der heisz- und kaltblütigen Tiere.'' Leipzig, p. 84.

———. 1830. (Verhdl. d. kaiser. Leopold-carolinisch Akad. d. Naturf. vol. 2; not seen.)

Causard, M. 1892. Sur la circulation du sang chez les jeunes araignées. C. r. Sci. Acad., 114: 1035.

———. 1896. Recherches sur l'appareil circulatoire des aranéides. Bull. sci. de la France et de la Belg., 29: 1.

Claparède, E. 1863. Études sur la circulation du sang chez les araignées du genre Lycose. Mém. de la Soc. de Physique et d'Hist. nat. de Genève, 17(i): 1.

CLARK, A. J. 1927. ''Comparative Physiology of the Heart.'' Cambridge, 157 pp.

CLAUS, C. 1878. Ueber Herz und Gefässystem der Hyperiden. Zool. Anz., 1: 269.

COKER, R. E. 1934. Reaction of some freshwater copepods to high temperatures. Jour. Elisha Mitchell Sci. Soc., Chapel Hill, 50: 143.

———. 1934a. Some aspects of the influence of temperature on copepods. Sci., 79: 323.

COLE, W. H., KAZALSKI, L. A., AND MCCOMAS, W. H. 1938. A perfusion solution for the lobster heart and the effects of its constituent ions on the heart. Bull. Mt. Desert Biol. Labor., p. 40.

CONANT, F. S., AND CLARKE, H. L. 1896. On the accelerator and inhibitor nerves to the crab's heart. Jour. Exp. Med., 1: 341.

CORNALIA, E. 1856. ''Monographia del Bombyce del Gelso.'' Mem. del reale Inst. Lombardo, Milano 5, p. 388.

COSMOVICI, N. L. 1925. Le coeur d'*Astacus fluviatilis* obéit-il a la loi de l'inexcitabilité périodique du coeur? C. r. Soc. Biol., 93: 797.

CROZIER, W. J., AND FEDERIGHI, H. 1925. Temperature characteristic for heart rhythm of the silkworm. Journ. Gen. Physiol., 7: 565.

———, AND STIER, T. B. 1927. Temperature characteristics for heart rate in embryos of *Limulus.* Proc. Soc. Exp. Biol. & Med., 24: 339.

———, AND ———. 1927a. Temperature and frequency of cardiac contractions in embryos of *Limulus.* Jour. Gen. Physiol., 10: 501.

———, AND ———. 1927b. Thermal increments for pulsation frequency in ''accessory hearts'' of *Notonecta. Ibid.,* 10: 479.

CUVIER, G. 1805. ''Leçons d'anatomie comparée.'' Paris, vol. 4, pp. 407–410.

———. 1817. ''La régne animale distribué d'aprés son organisation.'' Paris, vol. 2, p. 512.

DE CYON, E. 1900. Les tétanos du coeur. Journ. de Physiol. et de Pathol. génér., 2: 395.

DANILEWSKY, B. 1905. Ueber tetanische Contraction des Herzens des Warmblüters bei elektrischer Reizung. Arch. ges. Physiol., 109: 602.

DANN, M., AND GARDNER, E. M. 1930. Oxygen consumption of the cardiac ganglion of *Limulus polyphemus.* Proc. Soc. Exp. Biol. Med., 28: 200.

DELAGE, Y. 1881. Contribution a l'étude de l'appareil circulatoire des crustacés édriophthalmes marins. Arch. Zool. expér. génér., 9(i): 1.

———. 1883. Circulation et respiration chez les crustacés schizopodes (*Mysis* Latr.). *Ibid.,* 1(i): 105.

DESMARETS. 1825. *Cf.* Audouin and Edwards (1827).

DEZSÖ, B. 1878. Ueber das Herz des Flusskrebses und des Hummers. Zool. Anz., 1: 126.

DOGIEL, J. 1877. De la structure et des fonctions du coeur des crustacés. Arch. de Physiol. et Pathol., 4: 400.

———. 1877a. Anatomie und Physiologie des Herzens der Larva von *Corethra plumicornis.* Mem. Acad. St. Petersb., 24: 37.

———. 1894. Beitrag zur vergleichende Physiologie des Herzens. Arch. mikr. Anat., 43: 223.

DOHRN, A. 1866. Zur Naturgeschichte der Caprellen. Zs. wiss. Zool., 16: 245.

———. 1871. Zs. f. Med. u. Naturw. 6: 580; not seen.

DRENKELFORT, H. 1910. Neue Beiträge zur Kenntnis der Biologie und Anatomie von *Siphlurus lacustris* Eaton. Zool. Jb., Anat., 29: 527.

DRILHON, ANDRÉE. 1934. Sur le milieu intérieur des lepidoptères. C. r. Soc. Biol., 115: 1194.

DUBUISSON, M. 1928. Recherches sur la circulation du sang chez les crustacés. Arch. de Biol., 38: 9.

———. 1929. Des causes qui déclanchent et entretiennent les pulsations cardiaques chez les insectes. *Ibid.*, 39: 247.

———. 1930. L'état actuel de nos connaissances sur le rôle de la distension du muscle cardiaque dans l'activité du coeur chez les invertébrés. Arch. intern. de Physiol., 32: 416.

———. 1930a. New physiological studies on cardiac muscles of invertebrates. IV. The electrocardiogram of Limulus polyphemus. Biol. Bull., 59: 293.

———. 1930–31. Contributions a l'étude de la physiologie du muscle cardiaque des invertébrés. 6.—La contraction du coeur de *Limulus polyphemus* naît-elle en un point determiné de cet organe et se propage-t-elle aux autres segments par l'intermédiaire des nerfs cardiaques? Arch. intern. de Physiol., 33: 217.

———. 1930–31a. L'automatisme et le rôle du plexus nerveux cardiaques de *Limulus polyphemus.* *Ibid.*, 33: 257.

———. L'automatisme cardique dans la série animale. Bull. de la Classe des Sci., Acad. roy. de Belg., 17(v): 849.

———. 1933. "L'état actuel de nos connaissances sur la physiologie du muscle cardiaque des invertébrés." Paris, 130 pp.

ECKHARD, C. 1869. Mitteilung einiger die Herzbewegung betreffender Tatsachen. (In Eckhard's "Beitr. z. Anat. und Physiol," vol. 4, no. 2, p. 47.)

EDWARDS, A. M. 1872. Recherches sur l'anatomie des Limules. Ann. Sci. nat., 17(v): 25.

EDWARDS, D. J. 1920. Segmental activity in the heart of the *Limulus.* Amer. Jour. Physiol., 52: 276.

FISCHER, ED. 1918. Eine bei Raupen und Puppen beobachte Umkehrung der peristaltischen Herzbewegungen. Entom. Rundschau., Stuttgart, 35: 9.

FLORKIN, M. 1934. Sur la teneur en oxygène et en CO_2 du sang des insectes a système trachéen ouvert. C. r. Soc. Biol., 115: 1224.

FOX, H. M. 1921. Methods of studying the respiratory exchange in small aquatic organisms, with particular reference to the use of flagellates as an indicator for oxygen consumption. Jour. Gen. Physiol., 3: 565.

FREDERICQ, L. 1922. Action du milieu marin sur les invertébrés. Arch. intern. de Physiol., 19: 309.

———, AND VANDEVELDE, G. 1879. Physiologie des muscles et des nerfs du homard. Bull. Soc. roy. Belg. Classe des Sci., 47: 771.

FREUDENSTEIN, K. 1928. Das Herz und das Circulationssystem der Hönigbiene (*Apis mellifica* L.). Zs. wiss. Zool., 132: 404.

FRIES, E. F. B. 1926. Temperature and frequency of the heart beat in the cockroach. Jour. Gen. Physiol., 10: 227.

GAFFRON, E. 1885. Beiträge zur Anatomie und Histologie von *Peripatus.* (In Schneider's "Zool. Beitr.," 1: 145.)

GAMBLE, F. W., and KEEBLE, F. 1900. *Hippolyte varians*: a study in colour change. Quart. Jour. Micr. Sci., 43: 589.

GARREY, W. E. 1920. Dynamics of nerve cells. I. The temperature coefficient of the neurogenic rhythm of the heart of *Limulus polyphemus.* Jour. Gen. Physiol., 3: 41.

———. 1920a. II. The temperature coefficients of carbon dioxide production by the heart ganglion of *Limulus polyphemus. Ibid.*, 3: 49.

———. 1920b. The action of inhibitory nerves on carbon dioxide production in the heart ganglion of *Limulus. Ibid.*, 3: 163.

———. 1930. The pacemaker of the cardiac ganglion of *Limulus polyphemus.* Amer. Jour. Physiol., 93: 178.

———. 1933. The fractionate innervation of the myocardium of *Limulus polyphemus*—a disproof of myal conduction. Jour. Cell. & Comp. Physiol., 2: 355.

———, AND KNOWLTON, F. P. 1934–35. Peripheral neuromuscular augmentation in the heart of *Limulus polyphemus. Ibid.*, 5: 171.

GELFAN, S. 1931. Studies of single muscle fibers. III. Further evidence of graded responses in single fibers. Jour. of Physiol., 96: 16.

———, AND BISHOP, G. H. 1932. Action potentials from single muscle fibers. Amer. Journ. Physiol., 101: 678.

GEROULD, J. H. 1929. History of the discovery of periodic reversal of heart-beat in insects. Biol. Bull., 56: 215.

———. 1931. Premature reversal of heart-beat in *Bombyx.* Sci., 73: 323.

———. 1933. Orders of insects with heart-beat reversal. Biol. Bull. 64: 424.

GERSCHLER, W. 1910. Über ein Extremitätenorgan zur Regelung der Blutcirculation bei *Leptodora kindtii* (Focke). Zool. Anz., 36: 329.

VON HAFFNER, K. 1933. Die Mechanik der Blutbewegung bei *Phronima sedentaria.* Verh. deutsche zool. Gesellsch., 35: 183.

HAMILTON, M. A. 1931. The morphology of the water-scorpion, *Nepa cinerea* L. Proc. Zool. Soc. Lond., p. 1067.

HARVEY, W. 1628. "Anatomical studies on the motion of the heart and blood." (Engl. transl. by C. D. Leake, 1931; Springfield, Ill., 150 pp.)

HEINBECKER, P. 1931. Analysis of potential of *Limulus* medial cardiac nerve. Amer. Jour. Physiol., 97: 531.

———. 1933. The heart and the median cardiac nerve of *Limulus polyphemus*. *Ibid.*, 103: 104.

———. 1936. The potential analysis of a pacemaker mechanism in *Limulus polyphemus*. Amer. Jour. Physiol., 117: 686.

HENDERSON, J. T. 1927. A note on the effect of temperature on the cardiac rhythm of certain schizopods. Jour. Exp. Biol., 5: 135.

HERRICK, F. H. 1909. Natural history of the American lobster. Bull. U. S. Bur. Fish., 29, no. 747, 408 pp.

VON HERTWIG, R. 1900. ''Lehrbuch der Zoologie.'' Jena, 5th impr., 622 pp.

HIS, W. 1893. Die Entwicklung des Herznervensystems bei wirbelthieren. Abh. math.-phys. Classe sächs Gesellsch. Wissensch. 18: 1.

HOFFMANN, P. 1911. Über Electrokardiogramme von Evertebraten. Arch. f. Anat. u. Physiol., pp. 135–174.

———. 1911a. Das Elektrokardiogramm von *Limulus* im Chlornatriumrhythmus und bei Hemmung. *Ibid.*, pp. 175–180.

———. 1912. Ueber den Herzschlag des Fluszkrebses mit besonderer Berüchsichtigung des systolischen Stillstandes. Zs. f. Biol., 59: 297.

HOGBEN, L. T. 1925. Studies on the comparative physiology of contractile tissues. I. The action of electrolytes on invertebrate muscle. Quart. Jour. Exp. Physiol., 15: 263.

———, AND HOBSON, A. D. 1923–24. Studies on internal secretion. III. The action of pituitary extract and adrenaline on contractile tissues of certain invertebrata. Jour. Exp. Biol., 1: 487.

HOLLANDE, A. C. 1911. Du sang des insectes a hémorrhée et des insectes sans hémorrhée. Arch. Zool. expér. génér., 6: 283.

———. 1911a. L'autohémorrhée ou le rejet du sang chez les insectes. Arch. d'Anat. micr., 13: 171.

HOOKER, D. 1911. The development and function of voluntary cardiac muscle in embryos without nerves. Jour. Exp. Zool., 11: 159.

HOSHINO, N. 1925. Über die myogene Automatie des Limulusherzens. Arch. ges. Physiol., 208: 245.

HUNT, R., BOOKMAN, A., AND TIERNEY, M. J. 1897. Einige allgemeine Eigenshaften des Herzmuskels vom amerikanischen Hummer (*Homarus americanus*). Zbl. f. Physiol., 11: 274.

HUXLEY, T. H. 1878. ''A manual of the anatomy of invertebrate animals.'' New York, 596 pp.

HYDE, IDA H. 1906. A reflex respiratory center. Amer. Jour. Physiol., 16: 368.

IZQUIERDO, J. J. 1931. A study of crustacean heart muscle. Proc. Roy. Soc. Lond., 109B: 229.

JAHN, T. L., CRESCITELLI, F., AND TAYLOR, A. B. 1936. Electrical variations in the heart of the adult grasshopper (*Melanoplus differentialis*). Anat. Rec. 67, Suppl., p. 98.

JANET, C. 1906. Sur un organe non décrit du thorax des Fourmis ailées. C. r. Acad. Sci., 143: 522.

———. 1911. Sur l'existence d'un organe chordotonal et d'une vésicule pulsatile antennaire chez l'abeille et sur la morphologie de la tête de cette espèce. L'Apiculture, 55: 181.

JOLYET, F., AND VIALLANES, H. 1892. Recherches physiologiques sur le système nerveux accélérateur et modérateur du coeur chez le crabe. Ann. Sci. nat., 149(vii): 387.

KEIM, W. 1915. Das nervensystem von *Astacus fluviatilis* (*Potamobius astacus* L.) Ein Beitrag zur Morphologie der Dekapoden. Zs. wiss. Zool., 113: 485.

KLÖVEKORN, J. 1934. Das Organsystem der Blutbewegung bei *Gammarus pulex* L. Zs. wiss. Zool., 146: 153.

KNOLL, P. 1893. Über die Herzthätigkeit bei einigen Evertebraten und deren Beeinflussung durch die Temperatur. Sitzber. d. math.-naturwiss. Classe d. kaiser. Akad. der Wissensch., Wien, 102(iii): 387.

KOIDSUMI, K. 1928. On the heart contraction of the larvae of *Chironomus* and its temperature coefficient with special reference to the ''temperature characteristic.'' Dobutsugaku Zasshi, 40: 271; only abstract seen.

———. 1931. Thermal constant and the nature of the heart-beat of the larvae of chironomids and culicids. Jour. Soc. Trop. Agr., 2: 243.

KUWANA, Z. 1932. Morphological studies on the nervous system of the silkworm, *Bombyx mori* Linné. I. The innervation of the dorsal vessel. Bull. Imper. Sericult. Expt. Sta., Tokyo, 8: 109.

LANG, A. 1891. ''Text-book of comparative anatomy.'' Lond., vol. I, 562 pp.

LANGENDORFF, O. 1895. Untersuchungen am überlebenden Säugethierherzen. Arch. ges. Physiol., 61: 291.

LASCH, W. 1912–13. Einige Beobachtungen am Herzen der Hirschkäferlarve. Zs. allg. Physiol., 14: 312.

LOCY, W. A. 1884. Observations on the pulsating organs in the legs of certain Hemiptera. Amer. Nat., 18: 13.

LAPICQUE, L., AND LAPICQUE, MARCELLE. 1910. Action du curare sur les muscles d'animaux divers. C. r. Soc. Biol., 68: 1007.

———. 1936. Sur la curarisation chez les crustacés. *Ibid.*, 123: 388.

LATREILLE, P. A. 1831. Crustacea, Arachnida, and Insecta in Geo. Cuvier's ''Régne animale. . . .'' (New York, Engl. transl., vol. 3).

LEITCH, I. 1916. The function of haemoglobin in invertebrates with special reference to *Planorbis* and *Chironomus* larvae. Jour. Physiol. 50: 370.

VAN LEEUWENHOEK, A. 1688 ±, Engl. transl. 1816 by S. Hoole. ''The select works of Antony van Leeuwenhoek containing his microscopical discoveries in many of the works of nature. Translated from the Dutch and Latin editions by the author.'' Lond., vol. I, 314 pp., 10 pls.; vol. II, 344 pp., 20 pls., fo.

LEMOINE, V. 1868. Recherches pour servir a l'histoire des systèmes nerveux musculaire et glandulaire de l'écrevisse. Ann. Sci. nat. 9(v): 99.

LEONTOWITSCH, A. 1911. Über eine neue physiologische Untersuchungsmethode zum Studium der Blutzirkulation der Wirbellosen und einige Resultate derselben bei *Ranatra* und *Palaemon squilla*. Zs. allg. Physiol., 12: 337.

LÉVY, R. 1927. Mode de préparation de la daphnie permettant de faire battre son coeur en milieu artificiel. C. r. Soc. Biol., 97: 1600.

———. 1928a. Fonctionnement du vaisseau dorsal de la larve de mouche en milieu artificiel. C. r. Soc. Biol., 99: 1482.

———. 1928b. Action du potassium sur le vaisseau dorsal de la larve de mouche fonctionnant en milieu artificiel. *Ibid.*, 99: 1485.

LEYDIG, F. 1889. Ueber *Argulus foliaceus*. Arch. mikr. Anat., 33: 1.

LINDEMAN, V. F. 1928. The effect of various ions upon the heart rhythm of the crayfish, *Cambarus clarkii*. Physiol. Zool., 1: 576.

LOEB, J. 1899. ''Ueber Ionen welche rhythmische Zuckungen der Skelettmuskeln hervorrufen.'' Beitr. z. Physiol. Festschr., Prof. A. Fick, pp. 101–119.

LUND. 1825. *Cf.* Audouin and Edwards (1827).

LYONNET, P. 1760. ''Traité anatomique de la chenille qui ronge le Bois de Saule.'' La Haye, 616 pp., 18 pls.

MACALLUM, A. B. 1926. The palaeochemistry of the body fluids and tissues. Physiol. Rev., 6: 316.

MCCLENDON, J. F. 1905. On the anatomy and embryology of the nervous system of the scorpion. Biol. Bull., 8: 38.

MAGNUS, R. 1902. Die Thätigkeit des überlebenden Säugethierherzens bei Durchströmung mit Gasen. Arch. f. exp. Path. Pharm., 47: 200.

MALUF, N. S. R. 1933. Studies on the internal anatomy of the ''stink bug,'' *Nezara viridula* L. Bull. Soc. roy. entom. d'Egypte, 17: 96.

———. 1935. The myogenic automatism of the contraction of the heart of insects. Ann. Entom. Soc. Amer., 28: 332.

———. 1937. Unpublished data.

———. 1937a. Studies on the respiration of animals. I. Aquatic animals without an oxygen transporter in their internal medium. Zs. vergl. Physiol., 25: 1.

———. 1937b. II. Aquatic animals with an oxygen transporter in their internal medium. *Ibid.*, 25: 29.

MALPIGHI, M. 1669. ''Traité du Ver a Soie.'' (French transl. from the Latin by E. Maillot, 1878; Montpellier, 154 pp., 12 pls.)

MATSUKI, T. 1927. Observations on the heart beat in the *Chironomus* larva. Sci. Rept. Tohoku Imper. Univ., Biol., 3: 55.

MEEK, W. J. 1908. The relative resistance of the heart ganglia, the intrinsic nerve plexus, and the heart muscle to the action of drugs. Amer. Jour. Physiol., 21: 230.

MEYER, E. 1931. Über den Blutkreislauf der Ephemeriden. Zs. Morph. ökol. Tiere, 22: 1.

MOCQUART, F. 1883. Note sur un nerf cardiaque naissant des ganglions cerebroïdes chez la Langouste. Bull. Soc. philom. de Paris, 7: 65.

MOSELEY, H. N. 1871. On the circulation in the wings of *Blatta orientalis* and other insects, and on a new method of injecting the vessels of insects. Quart. Jour. Micr. Sci., 11: 389.

NELSON, J. A. 1924. The morphology of the honeybee larva. Jour. Agr. Res. 28: 1167.

NEWMAN, H. H. 1906. On the respiration of the heart. Amer. Jour. Physiol., 15: 371.

NEWMYWAKA, G. A. 1928. Zur Frage über die innervation des Herzens beim Fluszkrebses (*P. astacus* L.). Zool. Anz., 79: 209.

NEWPORT, G. 1918. ''Insecta.'' (In R. B. Todd's ''Cyclopaedia of anatomy and physiology,'' Lond., vol. 8, p. 981.)

———. 1843. On the structure, relations and development of the nervous and circulatory systems in Myriapoda and macrourous Arachnida. Philos. Trans. Roy. Soc. Lond., p. 243.

NUKADA, S. 1918. Ueber die Autotomie und die Koördination des Herzens. Biologische Untersuchungen über das Herz des *Limulus longispina*. Mitt. d. med. Fak. Univ. Tokyo, no. 19.

NUSBAUM, J. 1899. Beiträge zur Kenntnis der Innervation des Gefäszsystems nebst Bemerkungen über das subepidermale Nervenzellengeflecht bei den Crustaceen. Biol. Zbl., 19: 700.

OPOCZYNSKA–SEMBRATOWA, Z. 1936. Recherches sur l'anatomie et l'innervation du coeur de *Carausius morosus* Brunner. Bull. de l'Acad. polon. des Sci. et des Lettres, 2(B): 411.

PARHON, MARIE. 1909. Les échanges nutritif chez les abeilles pendant les quatres saisons. Ann. Sci. Nat., 9(ix): 1.

PATTEN, W. 1912. ''The evolution of the vertebrates and their kin.'' Philadelphia, 486 pp.

———, AND REDENBAUGH, W. A. 1899–00. Studies on *Limulus*. II. The nervous system of *Limulus polyphemus*, with observations on the internal anatomy. Jour. Morph. 16: 91.

PAUSE, J. 1918. Beiträge zur Biologie und Physiologie der Larve von *Chironomus gregarius*. Zool. Jb., allg. 36: 329.

PAWLOWA, M. 1895. Über ampullenartige Blutcirculationsorgane im Kopf verschiedener Orthopteren. Zool. Anz., 18: 7.

PICKERING, J. W. 1894. On the action of certain substances on the hearts of Daphniæ. Jour. Physiol., 17: 356.

PLATEAU, F. 1878. Sur les mouvements et l'innervation du coeur chez les animaux articulés. Bull. Acad. roy. de Belg., 46(ii): 203.

———. 1879a. Action of the heart of the crayfish. Nature, Lond., 19: 470.

———. 1879b. Les mouvements et l'innervation du coeur chez les crustacés. C. r. Assoc. Fr. Avanc. Sci., 7: 731.

———. 1880. Recherches physiologiques sur le coeur des crustacés decapodes. Arch. de Biol., 1: 595.

POGOSCHEWA, LYDIA. 1890. Die Nervenzellen der Scheeren und des Herzens vom Flusskrebs. Bote f. Naturwiss., St. Petersb., no. 5.

POLICE, G. 1902. Il nervo del cuore nello scorpione. Boll. Soc. nat. Napoli, 15: 146.

———. 1903. Sul sistema nervoso stomatogastrico dello scorpione. Archivio zoologico, 1: 179.

POLIMANTI, O. 1913. Beiträge zur Physiologie von *Maja verrucosa* M. Edw. I. Herz. Arch. f. Anat. u. Physiol., p. 117.

———. 1915. Physiologische Untersuchungen uber das pulsierende Gefäss von *Bombyx mori* L. I. Der Einfluss der Temperatur auf den Rhythmus des pulsierenden Gefäszes. Biol. Zbl., 35: 143.

———. 1915a. Untersuchungen über das pulsierenden Gefäsz von *Bombyx mori* L. II. Der Pulsrhythmus als Index der Wahrnehmung der Farben betrachtet. Zs. f. Biol., 65: 391.

POND, S. E. 1920–21. Correlation of the propagation-velocity of the contraction-wave in muscle with the electrical conductivity of the surrounding medium. Jour. Gen. Physiol., 3: 807.

POPOVICI-BAZNOSANU, A. 1905. Beiträge zur Kenntnis des Circulationssystems der Insekten. Jenaische Zs. f. Naturwissensch., 40: 667.

PORTER, W. T. 1905–06. Studies in the physiology of muscle. Amer. Jour. Physiol., 15: 1.

POTTS, F. A. 1932. (In Borradaile, L. A. and Potts, ''The Invertebrata,'' Cambridge, 645 pp.)

POWER, H. 1664. ''Experimental philosophy. In three books: containing new experiments (microscopical, mercurial, magnetical).'' Lond., 193 pp.

RABAUD, E. 1922. La saignée reflexe des coccinelles. Bull. Soc. zool. Fr., 47: 253.

RANVIER, L. 1880. ''Leçons d'anatomie générale.'' Paris, p. 63.

DE RÉAUMUR, R. A. F. 1734. ''Mémoires pour servir a l'histoire des insectes.'' Paris, vol. I, p. 643.

RETZIUS, G. 1890. ''Biologische Untersuchungen.'' Stockholm, neue Folge I, pp. 1–50, 14 pls.

RIJLANT, P. 1931. Étude a l'oscillographe cathodique du ganglion cardiaque de la limule polypheme. C. r. Soc. Biol., 108: 1144.

———. 1931a. Le courant d'action du coeur des crustacés, crab, homard, Bernard l'hermite. *Ibid.*, 108: 1147.

———. 1931b. L'oscillogramme cathodique du muscle cardiaque de la Limule polyphème. C. r. Séances de la Soc. Biol., 108: 825.

———. 1931c. L'activité du ganglion cardiaque de la Limule polyphème. *Ibid.*, 108: 828.

———. 1931d. Le phénomène de la conduction dans le coeur de la Limule polyphème. *Ibid.*, 108: 830.

———. 1931e. Le courant d'action du coeur des crustacés. Crabes, homard, Bernard l'hermite. *Ibid.*, 108: 1147.

———. 1931f. Les modalités de la réaction du coeur et du ganglion cardiaque isolé de la Limule polyphème a l'excitant électrique. *Ibid.*, 109: 33.

———. 1931g. Les automatismes du coeur de l'écrevisse. *Ibid.*, 109: 38.

———. 1933. L'automatisme cardiaque chez l'araignée: *Mygale, Epeira, Tarantula*, etc. *Ibid.*, 113: 917.

RITCHIE, A. D. 1932. Theories of muscular contraction. Nature, Lond., 129: 165.

ROBERTSON, T. B. 1906. Note on the influence of temperature upon the rate of the heart-beat in a crustacean (*Ceriodaphnia*). Biol. Bull., 10: 242.

ROBINSON, L. E., AND DAVIDSON, J. 1913. The anatomy of *Argas persicus*. Parasitol., 6: 217.

SAMOJLOFF, A. 1930. The extra systolic impulse of the ganglion of *Limulus* heart. Amer. Jour. Physiol., 93: 186.

SCHMITT, J. B. 1938. The feeding mechanism of adult Lepidoptera. Smithson. Misc. Coll., vol. 97, no. 4, 28 pp.

SHAFER, G. D. 1923. The growth of dragonfly nymphs at the moult and between moults. Stanford Univ. Publ., Univ. Ser. Biol. Sci., 3: 307.

SHIPLEY, A. E. 1909. Tardigrada. (In ''Cambr. Nat. Hist.'' vol. 4, Lond.)

SNODGRASS, R. E. 1925. ''Anatomy and physiology of the honeybee.'' New York, 327 pp.

———. 1935. ''Principles of insect morphology.'' New York, 667 pp.

SOLLMANN, T. 1905–06. The revival of the excised mammalian heart by perfusion with oil. Amer. Jour. Physiol., 15: 121.

STARLING, E. H. 1920. ''Principles of human physiology.'' Philadelphia, 1315 pp.

STIER, T. J. B., AND WOLF, E. 1932. On temperature characteristics for different processes in the same organism. Jour. Gen. Physiol., 16: 367.

STILES, W. 1930. Viscosity of protoplasm as determining the rate of biological reactions. Biol. Rev., 5: 171.

STRAUS-DURCKHEIM, H. E. G. 1828. ''Considérations générales sur l'anatomie comparée des animaux articulés, auxquelles on a joint l'anatomie descriptive du *Melolontha vulgaris* (Hanneton), donnée comme exemple de l'organisation des coleoptères.'' Paris, 434 pp.

SUZUKI, S. 1935. On the presence of ganglion cells in some crustacean hearts. Tohoku Imper. Univ. Sci. Repts., 10(iv): 417.

SWAMMERDAMM, J. 1669. ''The book of nature; or the history of insects.'' (Engl. transl. from the Dutch and Latin by T. Fllyod and J. Hill, 1758; Lond., pt. I, 236 pp.; pt. II, 153 pp., 53 pls.).

TAIT, J., AND BERRILL, N. J. 1936. Synchronism of heart and respiratory beat in *Limulus*. Amer. Jour. Physiol., 116: 153.

TAUBER, O. E., AND SNIPES, B. T. 1936. Velocity of hemocyte circulation in the elytron of the cockroach, *Periplaneta americana* Linn. Proc. Soc. exp. Biol. Med., 35: 249.

TCHAKHOTINE, S. 1935. Suppression de la fonction du coeur de la daphnie par la micropuncture ultraviolette. C. r. Soc. Biol., 119: 1392.

TENENBAUM, E. 1934. Der Ausfarbungsprozess in den Flugeldecken von *Epilachna chrysomelina* F. Arch. Entw.-mech., 132: 42.

THOMPSON, D. W. 1909. Pycnogonida. (In "Cambr. nat. Hist.," Lond., vol. 4.)

THOMPSEN, ELLEN (1938): Über den Kreislauf im Flügel der Musciden, mit besonderer Berücksichtigung der akzessorischen pulsierenden Organe. Zs. Morph. ökol. Tiere, 34: 416.

TIRELLI, M. 1936. Osservazioni sul ritmo e sul meccanismo delle inversioni circulatorie durante la metamorfosi di *Saturnia pavonia major* L. Archivio zool. ital., 22: 279.

TZONIS, K. 1936. Beitrag zur Kenntnis des Herzens der *Corethra plumicornis* Larve. Fabr. (*Chaoborus crystallinus* Geer). Zool. Anz., 116: 81.

VOGT, C., AND YUNG, E. 1894. "Traité d'anatomie comparée pratique." Paris, vol. II, 989 pp.

WAGNER, W. 1893. Étude sur l'activité du coeur chez les araignées. Ann. Sci. nat., Zool., 15: 311.

WALLING, E. V. 1908. The anatomy of the acrididaean heart and its histological structure. Kansas Univ. Sci. Bull., 4: 357.

WALTHER, A. 1898. Zur Lehre vom Tetanus des Herzens. Arch. ges. Physiol., 78: 597.

WEBER, E. H. 1846. Ueber Eduard Weber's Entdeckungen in der Lehre von der Muskelcontraction. Arch. f. Anat., Physiol. u. wiss. Medecin, pp. 483–527.

WEISMANN, A. 1874. Ueber Bau und Lebenserscheinungen von *Leptodora hyalina.* Zs. wiss. Zool., 24: 349.

WELSH, J. H. 1937. The eye-stalk hormone and the rate of the heart beat in crustaceans. Proc. Nat. Acad. Sci., Wash., 23: 458.

WHEDON, A. D. 1938. The aortic diverticula of the Odonata. Journ. of Morph., 63: 229.

WIGGLESWORTH, V. B. 1934. "Insect physiology." Lond., 134 pp.

WILLEM, V. 1917. Observations sur la circulation sanguine et la respiration pulmonaire chez les araignées. Arch. neerland. de Physiol., 1: 226.

———, AND BASTERT, C. 1918. Essais d'inscription des pulsations cardiaques chez une araignée. *Ibid.*, 2: 285.

WILLIS, T. 1674. "De anima brutorum. . . ." Amstelodami, 552 pp., 8 folded pls., 12 mo.

———. 1683. Engl. transl. of above work by S. Pordage. "Two discourses concerning the soul of brutes, which is that of the vital and sensitive in man." Lond., 234 pp., fo.

YEAGER, J. F. 1938. Mechanographic method of recording insect cardiac activity, with reference to effect of nicotine on isolated heart preparations of *Periplaneta americana.* Journ. Agr. Res., 56: 267.

———, AND HAGER, ANNA. 1934. On the rates of contraction of the isolated heart and malpighian tube of the insect, *Periplaneta orientalis*: Method. Iowa State College Jour. Sci., 8: 391.

———, HAGER, ANNA, AND STRALEY, J. M. 1935. Some physiological effects of certain aliphatic thiocyanates on the isolated heart preparation from the roach, *Blatta orientalis.* Ann. Entom. Soc. Amer., 28: 256.

———, AND GAHAN, J. B. 1937. Effects of the alkaloid nicotine on the rhythmicity of isolated heart preparations from *Periplaneta americana* and *Prodenia eridania.* Jour. Agr. Res., 55: 1.

———, AND HENDRICKSON, G. O. 1934. Circulation of blood in wings and wing pads of the cockroach, *Periplaneta americana.* Ann. Entom. Soc. Amer., 27: 257.

YOKOYAMA, T. 1927. Notes on periodic reversal of heart-beat in the silkworm *Bombyx mori.* Dobutsugaku Zasshi, 39: 45; only abstract seen.

YUNG, E. 1878. Recherches sur la structure intime et les fonctions du système nerveux central chez les crustacés décapodes. Arch. Zool. expér. génér., 7: 401.

———. 1879. De l'action principaux des poisons sur les crustacés. C. r. Acad. Sci., 89: 183.

ZAWARZIN, A. 1911. Histologische Studien über Insekten. I. Das Herz der *Aeschna*-larven. Zs. wiss. Zool., 97: 481.

ZEHNDER, H. 1934. Über die Embryonalentwicklung des Flusskrebses. Acta zoologica, 15: 261.

ZIMMERMANN, O. 1880. Über eine eigenthümliche Bildung des Ruckengefässes bei einigen Ephemeridenlarven. Zs. wiss. Zool., 34: 404.

ZOOND, A., AND SLOME, D. 1928. The relation of electrolytes to the cardiac rhythm of *Palinurus lalandii* and *Octopus horridus.* Jour. Exp. Biol., 6: 87.